Evolution of Self-organized Division of Labor in Social Insects

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Chapter 1

General introduction and thesis overview

General introduction

Division of labor is a complex phenomenon observed throughout nature. Theoretical studies have focused either on its emergence through self-organization mechanisms or on its adaptive consequences. We suggest that the interaction of self-organization, which undoubtedly characterizes division of labor in social insects, and evolution should be further explored. We review the factors empirically shown to influence task choice. In light of these factors,we review the most important self-organization and evolutionary models for division of labor and outline their advantages and limitations. We describe ways to unify evolution and self-organization in the theoretical study of division of labor and recent results in this area. Finally, we discuss some benchmarks and primary challenges of this approach. Division of labor was a concept first enunciated to refer to the partitioning of different tasks among individuals or groups of individuals in human civilized societies. Societies are composed of individuals specializing in different professions or trades. In industrialized societies, the degree of specialization of different individuals increased enormously. The early economist Adam Smith found division of labor to be root and consequence of mass production (Smith 1776). His classic example of the pin-making factory emphasized how the extreme specialization of individuals in small tasks that contributed separately to the making of individual pins allowed for an increase in productivity unachievable if each individual had to perform all the tasks involved in making the whole pin. Hence, division of labor means not only specialization of different individuals in separate tasks contributing to a whole, but also an increase in productivity arising from specialization and parallelization of tasks. Specialization, in this thesis, refers to the more frequent performance of a specific task or group of tasks by individuals, and does not per se imply an increase in the efficiency of task performance. In the models presented here, I always consider both specialization and its effect on productivity at the colony level. In nature, division of labor is ubiquitous and often associated with the evolutionary transition to higher levels of organization (Szathmáry & Maynard Smith 1995). For example, the transition from unicellularity to multicellularity was accompanied by a division of labor between germ cells and soma (Gavrilets 2010). Analogously, the transition from a solitary lifestyle to high degrees of sociality in insects was accompanied by the evolution of a sterile worker caste and a reproductive caste, which has led to the designation of eusocial insect colonies as super-organisms (Wilson 1971, Hölldobler & Wilson 1990). Just as we can find further division of labor in a multicellular organism with different organs and cell tissues, so can we find further division of labor among the sterile workers of a social insect colony, in the form of different behavioral and sometimes morphological worker castes taking over different tasks related to colony growth and maintenance (Oster & Wilson 1978). For example, while some workers tend to the brood and queen, others forage or defend the nest. The analogy with a multicellular organism ends here, though, as individuals in a social insect colony are not 100% related (contrary to cells in an organism), and thus much room for conflict exists between the sterile workers and the reproductive caste(Bourke & Franks 1995, Ratnieks et al. 2006). Furthermore, the level of specialization found in social insects is quite flexible (Oster & Wilson 1978). Even in species where individuals are morphologically differentiated and typically specialized in different tasks, the removal of individuals from one of the morphological castes is compensated by recruitment of individuals from another caste (Oster & Wilson 1978, Wilson 1985). What kind of behavioral mechanisms produce such specialization and flexibility at the same time? How do individuals know which tasks to perform? These are central questions in the study of division of labor. The main focus of my thesis is on the evolution of behavioral mechanisms leading to differentiation among individuals and to division of labor. Much is already known about biological factors influencing task choice, which I will briefly summarize here.

Biological factors affecting task choice

In several species of ants, workers differ morphologically, and can sometimes be grouped in discrete morphological castes. In other species, variation in morphology is continuous, or (in the majority of species) non-significant (Oster & Wilson 1978). Morphological differences typically reflect behavioral differences (e.g. Detrain & Pasteels 1991). For example, larger workers are more often seen engaged in nest defense and recovering large foraging items, whereas smaller workers typically do all other tasks. In some species, morphological differences serve a clear function. In honey pot ants, for example, a worker caste evolved that is typically bigger than the rest of the workforce and whose abdomens are gorged with food by other workers, to the point where they swell enormously (Hölldobler & Wilson 1990).

Morphological differentiation occurs only in a minority of species. More frequently, individuals differ in task choice according to their age, a phenomenon known as age or temporal polyethism. Young workers do in-nest tasks, whereas older workers perform tasks outside the nest, such as foraging (Oster & Wilson 1978). It has been argued that age polyethism is adaptive because leaving the riskier tasks to individuals with low survival probability (e.g., owing to physiological senescence) allows for higher overall colony productivity(Jeanne 1986a, Wakano et al. 1998). There is also some evidence that workers with shortened lifespan, due to injury or disease, start to forage earlier (reviewed in Tofilski 2009). In species of social insects where workers have functional ovaries, age polyethism may allow for young workers, whose reproductive value is higher, to maximize their direct fitness by staying close to the brood chambers.

There is also a genetic influence in the tendency to choose certain tasks. This has been particularly well worked out in the honey bee. Honey bee queens mate with multiple males, which means that the workers in a colony belong to different patrilines. It has been shown that workers from different patrilines have different tendencies to engage in pollen or nectar foraging, guarding and corpse removal, among other tasks (e.g. Robinson & Page 1988, 1989). However, in many social insect colonies, the degree of genetic variability is limited, as queens typically mate only once or twice. In species with limited genetic variability it is likely that other factors play a role in generating behavioral diversity. Recently it has been shown in ants that developmental conditions, such as temperature during pupation, affect the sensitivity of individuals for certain environmental cues, thus leading to behavioral differentiation between workers (Weidenmüller et al. 2009). Experience of adult individuals also affects their tendency to perform a task (Ravary et al. 2007).

The existing information reveals a plethora of factors influencing task choice, but not all social insect species possess the same characteristics. Despite that, behavioral specialization is frequently observed. Could there be a behavioral mechanism overarching all social insects, hence not requiring high genetic diversity, as caused by multiple mating, nor morphological differentiation?

Previous theoretical work has emphasized the role of self-organization in producing the type of specialized-yet-flexible behavior that characterizes social insects (Beshers & Fewell 2001). Self-organization is a process through which lower-level interacting agents, obeying to simple behavioral rules, produce seemingly complex patterns at the higher level (Kauffman 1993, Camazine et al. 2001). It has been suggested that self-organization may be an alternative force to natural selection, from which novel structures may arise (Kauffman 1993, Hoelzer et al. 2006). It is more likely, however, that natural selection may favor those self-organized patterns which are adaptive (Bonabeau et al. 1997, Camazine et al. 2001). Several self-organization models propose different mechanisms through which division of labor can emerge.

Theoretical models on division of labor

Recently I reviewed the existing self-organization and evolutionary models for division of labor (chapter 2 of this thesis). In brief, self-organization models may be considered to fall under three main classes: signal-response dynamics models, spatial differentiation models and social interactions models.

Signal-response dynamics models suggest that individuals differ in their responses to cues or signals of task need. Examples of cues of task need could be the number of larvae present, as a stimulus for brood care, or the amount of food stored, as a stimulus for foraging. Signals of task need would be for example, intensity of hunger signals in larvae or in nestmates (particularly in species where trophallaxis occurs). The idea pervasive to these models is that individuals that are more sensitive to certain stimuli will be more likely to engage in the corresponding task; if individuals differ in their sensitivity this may lead to specialization and division of labor. Among these models, the response threshold model (Bonabeau et al. 1996) is perhaps the most accepted among empiricists (e.g. Detrain & Pasteels 1991, O'Donnell & Foster 2001).

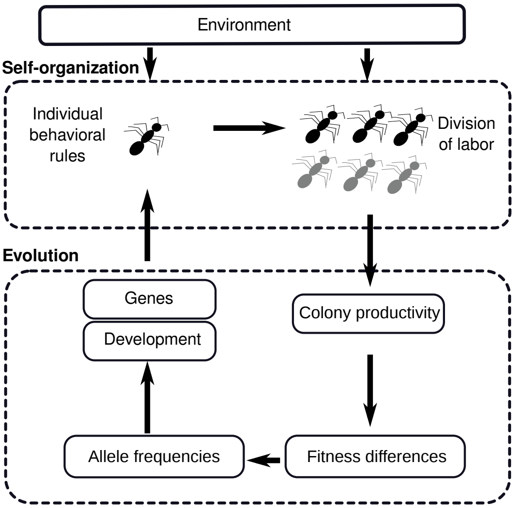

Figure 1.1: Schematic view of the integration of self-organization and evolution in a model for division of labor.

Spatial differentiation models assume that specialization among workers arises from the spatial location of tasks in the nest. According to these models, individuals remain at a location for as long as there is work to be performed there, after which they leave for the closest location where they perceive there is work to be done (Tofts 1993, Franks & Tofts 1994).

Social interaction models argue that individuals receive information from nestmates on their current task, and use this information to decide which task to perform. Workers are thus considered part of interaction networks, where information is transferred (Gordon et al. 1992, Pacala et al. 1996).

The behavioral rules explored in self-organization models are able to generate emergent specialization, for certain parameter values. However, the question remains of whether these behavioral rules can evolve, as well as the specific parameter values that generate specialization. The organization of work is determinant for the fitness of colonies (Gordon 1996), and it is therefore unlikely that natural selection is blind to it. The role of natural selection would be to shape the behavioral rules underlying task choice (Bonabeau et al. 1997), a point which has been largely neglected in self-organization models. There are models that focus on the adaptive value of division of labor, including in contexts outside social insects (e.g., Tannenbaum 2007, Wahl 2002), but these models largely ignore the behavioral mechanisms underlying division of labor. It is becoming more and more apparent that it is problematic to neglect behavioral mechanisms in evolutionary studies, since the course and outcome of evolution can strongly reflect these mechanisms (e.g., McNamara & Houston 2009). In general, there is still a lack of models that consider the evolution of behavioral mechanisms. In this thesis, I aim to contribute to fill this gap by integrating the self-organization and evolutionary perspectives on division of labor.

As illustrated in Figure 1.1, the integration of self-organization and evolution is relatively straightforward. Individuals interact among themselves and with the environment on an ecological time-scale, obeying to genetically encoded behavioral rules. From these interactions, a pattern of division of labor may emerge. On an evolutionary time-scale, natural selection will act to favor colonies whose behavioral rules produced the most adaptive outcomes, thus changing the allelic frequencies of genes underlying the behavioral rules.

Thesis overview

Chapter 2 is a review article where I argue in more detail that the integration of self-organization and evolution is necessary for a better understanding of division of labor. I review both the factors influencing division of labor in real social insects and the evolutionary and self-organization models developed to explain division of labor. I then explain the need for an integration of the two perspectives, and propose a way to model it, already briefly outlined above. I discuss the models that have already attempted an integrated perspective. Two of these models were developed during the course of my PhD and are here presented as chapters 3 and 5. Finally, I discuss the benchmarks that such an integrated approach should have, and challenges that may be encountered in the development of such models, such as the definition of a fitness function, the trade-off between realism of biological details and programming efficiency and the use of different measures of division of labor.

Chapters 3 to 5 consist of models using the modeling approach suggested in chapter 2. In all these models, I assume that populations consist of colonies, composed by a certain number of individuals. Colonies go through a work phase (where self-organization takes place) and then undergo reproduction, whereby the colonies that have accrued more fitness during the work phase produce a larger number of offspring. The offspring then found new colonies, starting a new generation. What varies between these models is the behavioral architecture underlying task choice. In **chapter 3**, I start from a well-known self-organization model, the fixed response threshold model (Bonabeau et al. 1996). In this model, individuals possess thresholds of response to task-associated stimuli. The original model considers a situation where individuals in a colony already belong to two different types, with opposing thresholds. It is not surprising under these circumstances for specialization to emerge. However, the question is whether such threshold distributions can evolve from scratch, and under what circumstances would they do so. As argued in chapter 2, an integrated approach allows for the evolution of parameters that underlie behavioral rules, in this case the thresholds. I allow for the evolution of thresholds in the presence and absence of costs to task switching. I also test whether it is possible to fine tune the distribution of workers over tasks according to specific proportions. In the light of the results obtained, I discuss the limitations of the response threshold model.

In **chapter 4**, I start out from another self-organization model, the reinforced threshold model (Theraulaz et al. 1998). In this model, response thresholds can change due to experience: successful task performance decreases the corresponding threshold, while not performing a task increases it. Here I allow for the evolution of the parameters governing threshold reinforcement, under different conditions of the effect of specialization in fitness. In a first, null-model, specialization has no effect on fitness. In the second scenario, there are costs to switching, as in chapter 2. In the third scenario, the efficiency of task performance increases with experience.

In **Box1** I address a potentially important modeling detail. When individuals are motivated to perform more than one task, there must be an algorithm in the model that allows them to choose one, i.e. a tie-breaking mechanism. I look at different ways to implement tie-breaking in a response threshold model, and briefly discuss how some of these methods may influence the level of division of labor observed.

In **chapter 5**, I maintain the aspects of the previous models related to population and within-colony dynamics, while allowing for more flexible behavioral architectures. The main objective of this chapter is to examine the effect of the behavioral architecture itself on the evolution of division of labor and the fine-tuning of division of labor to colony needs. For that I use evolving artificial neural networks (Yao 1999), where I allow the parameters of the networks to evolve. I employ both feedforward (where signals can only be passed forward in the network) and recurrent neural networks (where signals can be passed backwards, creating feedback loops within the network).

Chapter 6 is an empirical study which aims to test the hypothesis that different behavioral castes perceive environmental stimuli associated with tasks differently. Differences in stimulus perception could be generated at the antennal level, where olfactory receptors are located. I test antennae of nurses and foragers of the ant Camponotus fellah for detection of task-associated stimuli, such as the smell of larvae (associated to brood care), nestmates and non-nestmates (associated to nest defense), and a food-related odor (associated to foraging). For this purpose I use electroantennography, a simple electrophysiological technique.

Finally, in **chapter 7** I present a synthesis of the main results found and discuss potential future avenues of research, both from a modeling and empirical perspective.

Chapter 2

An evolutionary perspective on self-organized division of labor in social insects

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Abstract

Division of labor is a complex phenomenon observed throughout nature. Theoretical studies have focused either on its emergence through self-organization mechanisms or on its adaptive consequences. We suggest that the interaction of self-organization, which undoubtedly characterizes division of labor in social insects, and evolution should be further explored. We review the factors empirically shown to influence task choice. In light of these factors, we review the most important self-organization and evolutionary models for division of labor and outline their advantages and limitations. We describe ways to unify evolution and self-organization in the theoretical study of division of labor and recent results in this area. Finally we discuss some benchmarks and primary challenges of this approach.

Introduction

Division of labor is characterized by the performance of different tasks or roles by different groups of individuals. Early economists such as Adam Smith argued that the benefits of division of labor for industrialized societies included increased efficiency in task performance owing to specialization (exclusive dedication of individuals to specific tasks) and reduced costs of switching between tasks, thereby leading to overall higher productivity (Smith 1776).

In nature, division of labor, in the broad sense of the expression, is widespread. The main evolutionary transitions, such as those from prokaryotes to eukaryotes and from unicellular to multicellular organisms, were accompanied by division of labor (Szathmáry & Maynard Smith 1995). Within social groups division of labor is also common. In species with biparental care, males and females frequently have different roles in raising the offspring. In hornbills, for example, breeding females seal themselves in the nest and males must feed them during this time (Kemp & Woodcock 1995). Group hunting (e.g. Gazda et al. 2005), sentinel behavior in group foragers such as meerkats (Manser 1999), and specialization in either predator defense or provisioning in noisy miners (Arnold et al. 2005) are other examples of division of labor.

The most striking example of division of labor in non-humans occurs in insect societies. We focus on eusocial insects throughout this review owing to the abundant work in this area, although the general principles discussed are equally relevant for other social systems. In eusocial insects, such as honey bees, social wasps, ants, and termites, a few individuals monopolize reproduction (the queen caste), whereas the rest of the colony (the worker caste) performs tasks such as brood care, nest maintenance and foraging (Wilson 1971). The success of a colony is determined by its workers' ability to distribute themselves among tasks and to respond, as a group, to environmental conditions (Oster & Wilson 1978).

Division of labor also occurs among sterile workers. Similar to somatic tissues in a multicellular organism, workers can specialize in different tasks (Oster & Wilson 1978). Importantly the concept of specialization is a statistical one, reflecting an individual's tendency to perform particular tasks more often than others. The strength of this tendency may vary greatly, ranging from temporary behavioral differentiation to fixed morphological differentiation in insect species that form large societies (Robinson 1992).

Proximate analyses of division of labor generally are based on the concept of self-organization; according to this view, division of labor is an emergent property of the interaction of individuals obeying simple behavioral rules (Bonabeau et al. 1997, Page & Mitchell 1998). This concept has been supported by behavioral experiments showing that normally solitary seed-harvester ant queens and halictine bees exhibit task specialization when forced to associate, i.e. paired individuals dedicated most of their time to different tasks (Fewell & Page 1999, Jeanson et al. 2005, 2008). However, it is unlikely that such behavior would be evolutionarily stable if it occurred over many generations under natural conditions, as the performance of costly tasks that reduce individual fitness would be counter-selected. Hence, understanding the proximate mechanisms behind division of labor is not enough; we must also take into account the evolutionary trajectories (ultimate explanation) that selected these mechanisms.

The interplay of self-organization and evolution and the need for integration of the two perspectives have been recognized both inside and outside the scope of social insects (Corning 1995, Bonabeau et al. 1997, Page & Mitchell 1998, Richardson 2001, Halley & Winkler 2008). However, few models have attempted to unify these two approaches. In this review we outline suggestions to this end. We start by reviewing the empirical evidence on patterns of division of labor in social insects. We then classify existing self-organization models by the factors that create consistent individual differences in task choice in these models and summarize the most important evolutionary models for division of labor. We specify the reasons to integrate these self-organization models with an evolutionary perspective and identify the different benchmarks of evolved mechanisms underlying division of labor. Finally, we summarize the first insights obtained from such an integrated perspective and discuss future avenues of research.

Empirical background

In this section we first review the primary factors known to contribute to inter-individual differences in task choice. Then we discuss how colonies as a whole adjust to environmental changes as well as changes in the size and structure of the workforce.

Worker size and morphology

Worker size and morphology correlate with worker behavior in almost all species in which this has been studied (e.g., Wilson 1980, Detrain & Pasteels 1991, Robinson et al. 2009b). For example, in ants of the genus Pheidole with discrete morphological castes, the large “majors” are specialized in carrying large prey items to the nest but rarely engage in other tasks such as brood care, which is typically performed by the small “minors” (Wilson 1985, Mertl & Traniello 2009). It is not too surprising that morphologically differentiated castes behave differently (although empirical evidence indicates that behavior of such castes is flexible, to some extent, e.g., Detrain & Pasteels 1991). However, division of labor also occurs in the absence of such morphological differentiation, and these are the most interesting cases for this review.

Genetic variation

In species with multiply-mated queens such as honey bees and leaf-cutter ants, different patrilines differ in their tendencies to perform certain tasks (e.g., Robinson & Page

1989, Julian & Fewell 2004, Waddington et al. 2010; but see Fournier et al. 2008). Similar results were found for different matrilines in ant species in which colonies contain several queens (Snyder 1992, Blatrix et al. 2000) and in an experiment where broods of several queens were mixed within a single ant colony (Stuart & Page 1991). However, almost no information is available about whether the presence of several patrilines or matrilines within a colony is associated with a higher degree of specialization. Although increased within-colony genetic diversity may increase resistance to parasites (e.g., Baer & Schmid-Hempel 1999, Tarpy 2003, Wilson-Rich et al. 2009), there is little evidence that it leads to increased colony efficiency (Rosset et al. 2005, Fournier et al. 2008).

Developmental and nutritional factors

In many social insects, specialization strongly associated with the age of workers is observed, a phenomenon known as age polyethism (Wilson 1971, Oster & Wilson 1978). For example, young honey bee workers specialize in in-hive tasks, and then switch to foraging later in life. The transition from in-hive worker to forager is associated with physiological alterations, such as changes in juvenile hormone and vitellogenin titers, that correlate with age (Robinson 1987). Worker-worker interactions also mediate changes in hormonal titers, through transference of foraging-inhibiting substances (Huang & Robinson 1996, Leoncini et al. 2004). Nutritional state also plays a role in behavioral differentiation and interacts with developmental hormones and the insulin-signaling pathway (Schulz et al. 1998, Amdam et al. 2003, Page & Amdam 2007, Ament et al. 2008).

External factors such as temperature, light and humidity during development may also affect task preferences. In the ant *Camponotus rufipes*, temperature during larval development influences the response of individuals to thermal stimuli at the adult stage (Weidenmüller et al. 2009), which causes inter-individual differences in tendency to move brood at certain temperatures. Other external factors (e.g., light and humidity) remain to be investigated as sources of variation in task preference.

Individual experience

Individual experience influences task preference in the thelytokous (females are produced from unfertilized eggs) ant *Cerapachys biroi* (Ravary et al. 2007). In individuals of the same age cohort, foraging tendency was positively correlated with exposure to successful foraging experiences in the past. Behavioral differentiation of individuals thus resulted from experience alone. It would be interesting to investigate whether a similar pattern occurs in non-thelytokous species.

Interactions with the environment

Social insect colonies have a strong ability to overcome environmental perturbations by changing the number of workers engaged in specific tasks. In harvester ants, the number of foragers shifts as a response to predation risk (Mackay 1982, Munger 1984) or changes in resource availability (Gordon 1991, Schafer et al. 2006). Colonies of the ant *Pheidole morrisi* respond to seasonal fluctuations in food availability both by individually increasing fat storage and by increasing the number of workers in the replete caste (Yang 2006).

In many species whole colonies readily migrate when the current nest location is damaged or a better location is found. This complex process is similar in honey bees and several ant species (reviewed in Visscher 2007): First, a few individuals scout for new nest sites; second, one location is chosen through quorum sensing Pratt et al. 2002, Pratt 2005, Seeley & Visscher 2003; and third, the whole colony moves to the new location.

Social interactions are crucial to efficiently react to environmental change. Depending on species active workers can use chemical signals or direct physical contact to recruit inactive workers. Contact with successfully returning foragers influences the decision of ants in the nest to forage or not in several species (Gordon & Mehdiabadi 1999, Greene & Gordon 2003, 2007). Foraging honey bees, upon returning to the nest, must search for food-storer bees that unload and store the nectar collected. The time spent searching for food-storer bees has been shown to be used by foragers to regulate foraging rates; short search times elicit the recruitment of more foragers (Seeley & Tovey 1994). The modulation of division of labor by worker-worker interactions thus appears to allow for efficient use of the information acquired by all workers in the colony.

Colony size and life-cycle

Eusocial insect colonies typically go through three different phases in their life-cycle: a founding stage in which new nests are founded by recently mated queens (and kings, in case of termites), an ergonomic growth stage in which the colony produces workers only and increases in size, and a reproductive stage in which the colony produces new sexuals (males and gynes) (Oster & Wilson 1978). The transition from ergonomic growth to reproduction is generally marked by the attainment of a certain colony size, which varies from species to species.

In species with morphological castes, often in the initial founding stage the queen produces only small workers ("minims") and as the colony grows, the average worker size increases (Hölldobler & Wilson 1990). Throughout the lifetime of a colony the need for some tasks such as nest building and foraging should drastically change, although the need for other tasks such as maintaining temperature and humidity conditions should remain similar. In *Lasius niger* ants, different proportions of workers are engaged in particular tasks over the growth of the colony (Mailleux et al. 2000). However, to our knowledge no empirical study has measured the extent of changes in task need with colony growth.

Colony size has been argued to influence the complexity of social behavior and division of labor; smaller colonies should have more generalist workers (Karsai & Wenzel 1998, Bourke 1999, Anderson & McShea 2001). For example, in the ant *Rhytidoponera metallica*, large colonies show pronounced age-based division of labor whereas small colonies do not (Thomas & Elgar 2003). In the ant *Temnothorax albipennis*, large colonies have larger proportions of brood-carrying specialists than small colonies (Dornhaus et al. 2008). However, there are no differences between large and small colonies in a standardized measure of division of labor (Dornhaus et al. 2009).

Models for self-organized division of labor

Self-organization models attempt to explain the division of labor at the colony level by using simple individual behavioral rules that assume neither complex cognitive abilities nor centralized control. We classify these models into three groups on the basis of the factors underlying the emergence of individual differences in task choice, namely, signal-response dynamics, spatial differentiation of tasks, and social interactions.

Signal-response dynamics

These models assume that individuals differ in their response to environmental signals of the colony's need for specific tasks. Possible signals include pheromones emitted by larvae to elicit care from workers, nest temperature, or the amount of stored food. The models further assume that these signals are dynamic; signals increase in intensity in the absence of sufficient task performance, and decrease with a certain level of task performance (Figure 2.1a).

The fixed threshold models assume that each individual has thresholds for particular tasks that are constant over time. Thresholds determine the intensity of signal needed for the individual to respond (Bonabeau et al. 1996, 1998, Page & Mitchell 1998, Graham et al. 2006, Jeanson et al. 2007, Gove et al. 2009). If signal intensity lies above an individual's threshold, the individual will perform the task. If signal intensity lies below the individual's threshold, the individual will not perform the task. The feedback between task performance and signal intensity allows for consistent inter-individual differences to be expressed: Individuals with lower thresholds for a task decrease the signal for that task, thereby decreasing the probability that individuals with higher thresholds will ever perform it. However, individuals may eventually perform tasks for which they have high thresholds, in the absence of workers with lower thresholds. Hence, both task specialization and flexibility can be emergent outcomes of the model's dynamics.

The reinforced threshold model uses the same concept, with the difference that individual thresholds can change owing to experience (Plowright & Plowright 1988, Theraulaz et al. 1998, Gautrais et al. 2002). Performance of a task decreases the corresponding threshold, whereas not performing a task results in an increase of the threshold.

The empirical support for a response threshold-like mechanism comes from studies of thermoregulation in bumble bees and ants in which different individuals consistently started to perform thermoregulatory behaviors at different temperatures (O'Donnell & Foster 2001, Weidenmüller 2004). Thresholds likely have a genetic or developmental basis, because different genetic lineages as well as morphological castes generally differ in their tendency to respond to task-associated stimuli (Detrain & Pasteels 1991, Pankiw et al. 1998, Page et al. 1998). Ravary and coworkers (2007) provide empirical support to the threshold reinforcement model.

Owing to our lack of knowledge about the actual dynamics of task stimuli in real colonies, the implementation of task stimuli in signal-response models is simplistic. Many of these models assume a linear increase in task stimulus in the absence of work and a linear decrease with the amount of work performed on the task, but stimulus increase or decrease will almost certainly be nonlinear in a real-world setting. The nature of tasks may also differ: Some tasks require the maintenance of the stimulus within certain bounds (homeostatic tasks, e.g., thermoregulation), whereas for other tasks it is adequate to keep the stimulus at the lowest level (maximizing tasks, e.g., foraging). The type of tasks present may influence the extent to which workers should specialize or generalize (Johnson 2003).

Spatial differentiation

The foraging-for-work model (Tofts 1993, Franks & Tofts 1994) suggests that the spatial distribution of tasks could lead to inter-individual differences in behavior. In this model, tasks are spatially distributed similarly to a production line. Individuals at each location process and pass along items coming from an external source until the items reach the final task in the line (Figure 2.1b). This idea takes inspiration from real colonies in which individuals forage, cut up food items and transport them back to the colony, where finally the food items are fed to the brood.

The algorithm of task choice in the standard versions of the foraging-for-work model (Tofts 1993, Franks & Tofts 1994) requires that individuals actively look for another task if they fail to pass an item to the subsequent task or if they fail to receive items from the preceding task. At the equilibrium state, workers stay in the same task for a prolonged time. By including in the model a certain rate at which individuals are born and introduced into the workforce at the last task in the production line (analogous to brood care) and a maximal age after which workers die, age polyethism emerges. This is due both to the fact that younger workers displace older workers in their task and to the assumption that tasks are spatially distributed in a sequence.

The foraging-for-work model aims to show that task-choice need not be state or age-dependent for age polyethism to occur. The assumption that all workers have equal tendencies to perform every task has encountered some criticism (Robinson et al. 1994, Traniello & Rosengaus 1997) because much evidence has been found both for genetic and physiological correlates with task choice (see page 18). Recent evidence also indicates that young workers are able to do fewer tasks than older workers (Seid & Traniello 2006).

Social interactions

Interaction models explore the role of social interactions as the driving mechanism behind division of labor. Interactions among workers lead to shifts in their behavioral state and task choice (Figure 2.1c). The models differ in the information exchanged during interactions.

Gordon et al. (1992) assume that workers, via social interactions, receive information about tasks performed by others. By comparing the perceived task distribution with an intrinsic desired task distribution, individuals switch tasks in the case of a mismatch between the two distributions. As a result, an equilibrium is reached in which workers distribute themselves according to the intrinsic task distribution.

Pacala et al. (1996) develop a model in which the profitability of tasks changes with time. By comparing the perceived profitability of others with the profitability of their own task, workers decide whether to switch to a more profitable task. If profitability is proportional to colony efficiency, this process leads to a colony that is able to track environmental variation, thereby maintaining an efficient distribution of workers over tasks.

Other models address more specifically the division of labor between nest workers and foragers, as well as its modulation by inhibitory interactions between the two types of workers (Naug & Gadagkar 1999, Beshers et al. 2001). These models find that a simple social activation-inhibition mechanism can explain the pattern of age polyethism often found in eusocial insects.

Limitations of current self-organization models

By demonstrating that emergent specialization is possible through simple mechanisms, self-organization models serve as a proof of principle that high cognitive processes are not required to achieve complex group behavior. However, these models typically do not consider the evolutionary trajectories that may lead to division of labor. This also holds for those self-organization models that implicitly incorporate adaptive reasoning. For example, in social interaction models, task choice algorithms are designed to favor tasks for which there is a higher need. However, the question of why and how individuals are endowed with an intrinsic knowledge of colony needs is not addressed. Without a clear idea of how natural selection shaped the task choice mechanism underlying a self-organization model, our understanding of self-organized division of labor remains incomplete. Bonabeau et al. (1997, p. 191) stated: "… natural selection, operating on parameters that modulate individual and colony-level properties, has certainly picked the forms of self-organization that we see in social insects because they are adaptive or cooperative". However, disappointingly few attempts have been made to develop re-

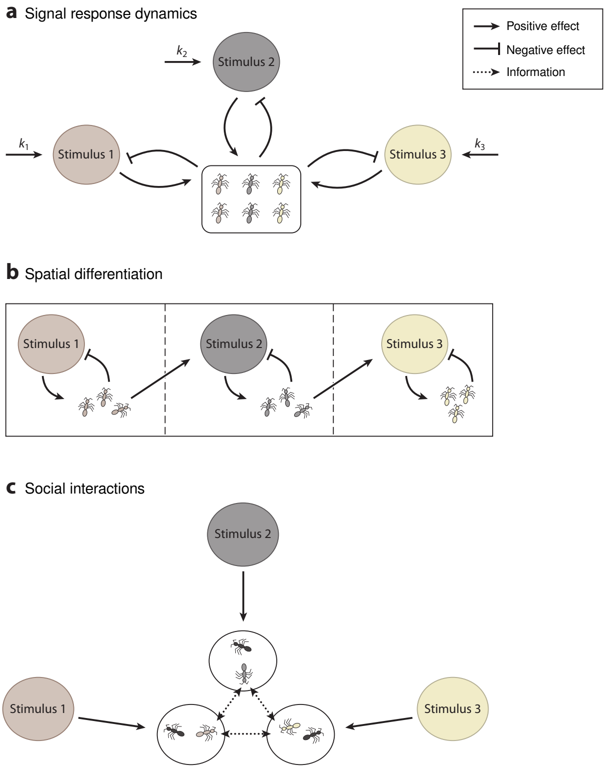

Figure 2.1: Schematic representation of the main factors contributing to interindividual variation in self-organization models of division of labor. (a) In signal-response models, the number of active workers increases with the amount of stimulus (increasing by k over time), and active workers reduce the stimulus level, decreasing the need for more workers to become active. Intrinsic differences in workers, such as response thresholds, are indicated by different colors. (b) Spatial differentiation of tasks (and of the associated stimuli) leads to different individual behavior in the foraging-for-work model (drawn from information in Tofts 1993). Local stimulus determines the number of active workers for each task (curved arrows). Task-related items are processed and passed on from one task-group to another (straight arrows), promoting the increase of stimulus at the different locations. Workers active for different tasks are indicated in different colors. (c) In social interaction models, the decision of workers to perform different tasks is affected not only by the associated stimuli (solid arrows) but also by information received from other workers (dashed arrows). Workers active for different tasks are indicated in the colors of the corresponding tasks. Idle workers are depicted in black.

alistic scenarios for how the mechanisms underlying self-organized division of labor evolve over the course of generations.

Evolutionary models of division of labor

Optimal caste ratios

The first generation of evolutionary models for division of labor applied optimality principles to understand the distribution of castes and tasks in a colony. In their classical book, Oster & Wilson (1978) derived optimal caste ratios in a situation in which morphological differences influenced the efficiency with which individuals couldperform various tasks. They offer two primary theoretical explanations for the observation that in social insects fewer castes than tasks exist: First, production of a broad variety of physical castes is costly at the colony level; second, the behavioral flexibility of castes allows the colony to react more rapidly to environmental changes.

Oster & Wilson's view of caste ratios as an adaptive trait has been challenged by empirical studies that consistently fail to find correlations between colony productivity and caste ratios (for a review see Schmid-Hempel 1992). The behavioral flexibility of workers is considered to be the main factor responsible for adjustment of the worker force to changing environments, including different ratios of morphological or age castes (Gordon 1996). Nevertheless, the question still remains of whether the existence of different morphological castes actually increases fitness and, if so, why morphological castes are not found more often.

Adaptive specialization

Any form of specialization may be beneficial for two reasons (Smith 1776): First, it may allow for higher individual efficiency, (e.g., owing to training or through gains in task-specific information); second, specialization may reduce the costs of switching tasks (e.g., time lost traveling between task locations or energy costs owing to shifts in behavioral state). Several evolutionary models of division of labor have investigated the conditions under which a task-specialist strategy is favored over a task-generalist strategy.

Wakano and co-workers (1998) developed an age polyethism model in which workers were grouped into different age classes. Each age class allocated labor in predetermined proportions for inside (e.g., brood care) and outside (foraging) tasks. In a situation in which outside tasks incurred higher mortality risk and thus worker life expectancy decreased with age, it was found that a "strict" age polyethism (with young workers specializing in inside tasks and older workers specializing in outside tasks) was adaptive. Furthermore, environmental fluctuations affected the type of age polyethism that was optimal: When large fluctuations alter the efficiency of both inside and outside workers, a smooth transition from performing inside to outside tasks is optimal. When fluctuations affected only foraging, a sharp transition was favored.

Several other models have been proposed to explain division of labor in systems other than social insects. Wahl (2002) formulated simple game-theory models to study division of labor in co-viruses, in which different types of virions co-infect a host cell and perform complementary tasks in the replication process (Nee 1987). In these models, phenotypes were fixed: Individuals could either perform only one of the tasks (specialists) or have the ability to perform all tasks (generalists). If all tasks were performed, individuals shared the resulting benefits. Wahl made two types of assumptions concerning the costs associated with task performance. She found that when costs were paid mainly for the ability to perform a task (fixed costs), rather than with the performance itself (marginal costs), the outcome was a polymorphic population of specialists, i.e., individuals who could perform complementary tasks. When costs were paid for task performance only, a combination of generalists and specialists for one task was optimal.

Although Wahl's models were inspired by a different context, some parallels to social insects can be drawn. In social insects we could consider as fixed the costs involved in developing particular morphological or physiological structures, or the costs involved in switching tasks. These are costs that individuals pay for the ability to perform a task. Marginal costs would be, for example, the energy expenditure involved in task performance. From Wahl's results, one could thus predict that separate groups of specialists should frequently evolve when fixed costs are involved, such as the costs of developing features such as strong mandibles or storage organs.

Another model for studying the adaptive value of specialization takes inspiration from enzyme-substrate reactions. Tannenbaum (2007) compared the productivity of systems in which binding and processing a resource to release a final product could be performed through an undifferentiated pathway (generalist strategy) or a differentiated pathway (specialist strategy). For a low density of agents, undifferentiated pathways were favored owing to the costs of transferring products between specialists. In a resource-limited regime, a differentiated pathway was more productive than an undifferentiated pathway when the specialist enzymes were more efficient at binding to the incoming resource and process intermediate. When resource availability was high, the differentiated pathway became more productive when it could process faster the molecules to which agents were bound. These results are quite intuitive because at low densities, transferring the products of tasks among specialists becomes less efficient, and hence division of labor is selected against. In social insects this should translate into less marked division of labor in smaller colonies, as indeed seems to be the case (Thomas & Elgar 2003).

Limitations of current evolutionary models

The main limitation of current evolutionary models is that they tend to ignore the mechanisms through which specialization may arise. Using a fixed set of strategies, these models use fitness and productivity measures to test when specialization is better than a generalist strategy. Much like self-organization models implicitly assume evolutionary adaptation, evolutionary models assume that some mechanism will evolve that allows for adaptive behavior. The ability to evolve specialization, however, may be strongly dependent on the mechanism through which it arises. Furthermore, the analysis of only a fixed set of strategies is limiting. A better approach would be to allow the set of strategies to evolve itself, thereby alleviating the constraints on adaptive evolution.

Specialization is the crucial defining property of division of labor. Evolutionary models are usually based on the (plausible) assumption that worker specialization enhances the productivity of a colony because of synergistic effects. However, surprisingly little information is available on how specialization increases productivity. Moreover, the information available does not suggest a close correlation between individual efficiency in task performance and specialization (Dornhaus 2008, Muscedere et al. 2009).

Unification of self-organization and evolutionary models

In our view, self-organization and evolutionary models are not contradictory in any way, and in fact they can (and should) be integrated into a common framework. One way to do this is illustrated in Figure 2.2. The figure shows that it is useful to distinguish between two timescales: a short-term timescale at which interactions take place (corresponding to the life of a colony), and a long-term timescale at which evolutionary changes occur. On the short-term timescale, self-organized division of labor emerges as a result of the behavior of individuals, who obey to inherited behavioral rules. Division of labor then has a direct relationship with productivity of a colony and fitness (number of reproductives). On the long-term timescale, fitness differences between colonies lead to a change in allele frequencies, and hence in the genetic make-up of individuals, eventually changing the rules underlying division of labor.

A first approach is to consider various task choice algorithms, implement a measure of colony fitness, and allow for selection among the algorithms. A good example of this approach is the model of Waibel et al. (2006). They implemented a task allocation model in which colony performance increased with the number of workers engaged in each task. Different task choice algorithms were studied and their underlying genes were allowed to evolve under different conditions of intra-colonial genetic relatedness and environmental perturbations. Under environmental perturbations and high relatedness, a more flexible algorithm that took both individual preferences and the behavior of colony members into account performed best. Unfortunately, the implications of this model for division of labor cannot be evaluated because individual levels of specialization were not reported.

In a similar study Tarapore et al. (2009) implemented an evolutionary version of the fixed response threshold model in which thresholds were allowed to evolve in order to study the genetic architecture and mating system in a task allocation scenario. Individuals could perform a foraging task and a regulatory task; fitness benefits from the foraging task accrued only when the regulatory task was within certain bounds. The colonies achieving the highest performance in each generation contributed to the next generation in proportion to their fitness. The results of this study indicate that variation in thresholds is a main determinant of colony productivity. Hence, colony performance was influenced by the number of males queens mated with as well as the number of loci encoding the response thresholds.

Duarte et al. (in press) (chapter 3 of this thesis) also implemented an evolutionary version of the fixed response threshold model, where the evolutionary trajectories of the thresholds were explicitly followed. The model studied the effect of the evolution of thresholds on division of labor, colony fitness and work distribution. This study demonstrated that specialization could evolve if switching among tasks involved high costs. If this was the case, a previously homogeneous population evolved to a multimodal distribution of thresholds (via evolutionary branching), and differentiation of thresholds allowed for division of labor. However, only colonies with an adequate combination of thresholds exhibited pronounced specialization. The branching of thresholds also can be interpreted as the evolution of separate morphological castes in which individuals of a caste behave as specialists if enough individuals of the other caste are present, as also observed in empirical data (Wilson 1985).

The above models are limited because they take an existing self-organization model (such as the response threshold model) as their point of departure. This imposes limitations upon the mechanisms that can potentially evolve and therefore constrains the path of evolution. For example, in the model by Tarapore et al. (2009), individuals generally evolved low thresholds for the regulatory task, whereas thresholds for the foraging task were highly variable among individuals. Hence, when the stimulus for the regulatory task was low, workers with a high threshold for the foraging task remained idle. Thus, colony efficiency was constrained by the inability to evolve thresholds that minimize idleness for a given task independent of the stimulus level for the other task. Similarly, Duarte et al. (in press) noticed that the standard implementation of the fixed-threshold model always leads to a uniform distribution of workers over tasks, even if a skewed distribution is more adaptive. In fact, the distribution of workers over tasks was largely independent of the location of the thresholds; it instead was determined by the parameters governing the stimulus dynamics.

A possible way to circumvent the limitations of *a priori* mechanisms is to investigate the evolution of more flexible task choice mechanisms. One interesting option is neural network modeling, which is applied regularly in evolutionary robotics and has offered interesting insights into the evolution of behavioral strategies such as communication and cooperation (Perez-Uribe et al. 2003, Floreano et al. 2007, Mitri et al. 2009,

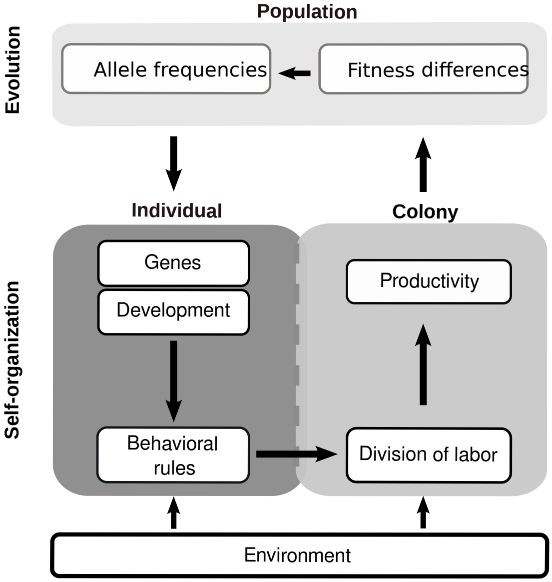

Figure 2.2: Integration of self-organization and evolution in a coherent framework. On a short-term timescale, self-organization takes place. The factors influencing task choice at the individual level (i.e., genetics, development, and environment – abiotic and biotic, including social interactions) interact to produce the individual phenotype, the rules through which individuals self-organize to divide labor. The colony's behavior, and its interaction with the environment, has an effect on productivity and hence on fitness. On the long-term timescale, natural selection acts on the existing variation in fitness at the population level, thereby changing allelic frequencies of the genes underlying the rules for self-organized behavior.

Floreano & Keller 2010, Mitri et al. 2011). Neural networks can be used to simulate the processing of stimuli by an individual through receptor cells connected to output cells controlling behavioral responses (Figure 2.3) (Ghirlanda & Enquist 1998). Even for relatively small neuronal networks, the number of potential stimulus-response patterns (which form the substrate for evolution) is almost limitless. All kinds of behavioral architectures can evolve, whereas in traditional models the behavioral bauplan is determined by the modeler *a priori*. On the downside, the evolution of neural networks is not always efficient, because fitness optima have to be found in a high-dimensional trait space. Moreover, the interpretation of the functioning of an evolved network is not always straightforward.

Two recent studies apply network modeling to the evolution of self-organized division of labor. Lichocki and colleagues (2012) considered a network version of Tarapore et al.'s (2009) model for combining a foraging and a regulatory task. They showed that the efficiency of task allocation and overall colony productivity were greatly improved when a simple neural network controlled individual decisions. In the evolved networks, the link between the stimulus for one task and the likelihood of performing the other task was partly decoupled. As a result, fewer workers were idle, which lead to higher colony efficiency.

In the same vein, in the model of Duarte et al. (2012) (chapter 5 of this thesis), a neural network approach allowed for worker distribution over tasks to be more flexible than with the fixed response threshold model. This study also investigated a slightly more complex network that allows past experience to affect individual behavior. Specialization mediated by individual experience evolves easily when switching tasks bears costs to the colony.

Benchmarks of evolved mechanisms underlying division of labor

In this section we highlight some desirable features that a unifying model for the evolution of self-organized division of labor should include. We discuss these features in light of existing models and suggest future avenues of research.

Emergent specialization and adaptive distribution of workers

Because emergent specialization at the individual level is the most obvious property of division of labor, we are interested in those systems in which selection favors the establishment of specialization. Specialization may be selected directly, if it brings an immediate advantage, or indirectly, if the behavioral rules leading to specialization are selected owing to other beneficial consequences.

Specialization is easy to obtain in self-organization models, but it may be unstable when studied from an evolutionary perspective. For example, in the model of Duarte et al. (in press), selection for maximum colony performance often drives thresholds to zero level. As a result, specialization vanishes, even if it is beneficial for colony productivity.

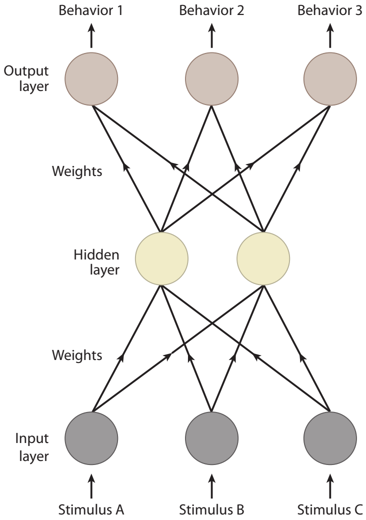

Figure 2.3: Example of a simple feed-forward neural network. Environmental stimuli are perceived by neurons at the input layer and passed on as signals to the hidden layer, where they are further transformed. Finally, the signal reaches the output neurons, where a decision is made regarding which task to perform. The network has many parameters, such as connection weights (arrows), that can be positive or negative and influence the strength of the signal. These parameters are allowed to evolve.

For the proper functioning of the colony as a whole, an evolved mechanism for division of labor should produce an adaptive distribution of workers over tasks. As shown by Duarte et al. (in press), the standard version of the response threshold model does not have this property, because it always leads to a uniform distribution of workers over tasks. Hence, a more sophisticated modeling set-up is required (such as neural network modeling; Duarte et al. 2012) to enable the evolution of an asymmetric distribution in which some tasks are performed by a larger proportion of workers whereas other tasks require fewer individuals.

Flexibility and developmental robustness

Any realistic model for the evolution of division of labor should allow for flexibility in colony behavior, that is, the ability to cope with environmental challenges necessitating a change in the distribution of workers over tasks. Thus far few models addresses such flexibility (e.g., Tofts 1993, Pacala et al. 1996), but even in these models it is unclear how workers acquire knowledge about how which tasks to prioritize over time. There is an urgent need for models exploring the implications of temporal variation (e.g., seasonal variation in food abundance).

The ability to cope with environmental challenges necessitates robustness with respect to the internal state of the colony. An adequate timing of task performance and an optimal distribution of workers over tasks should be attained irrespective of factors such as within-colony genetic variability, colony demographic structure, or the developmental dynamics of a colony (see Tarapore et al. 2009). Developmental plasticity that allows the generation of phenotypic diversity in colonies with low genetic diversity has not yet received the attention it deserves.

Evolutionary attainability and stability

It is now well established that in social evolution seemingly favorable traits (such as a mechanism that generates division of labor) are not necessarily attainable, because selection may drive a population away from these solutions ("Garden of Eden" scenarios; Nowak 1990). Even if a seemingly favorable trait is attained, it is not necessarily evolutionarily stable (Maynard Smith 1982). Examples of inaccessible or evolutionarily unstable traits abound in situations with evolutionary conflicts or counteracting selection at different levels of organization (McNamara & Weissing 2010). Both factors are relevant in colonies of social insects.

Members of a colony may have conflicting interests regarding caste fate of female brood, relative colony investment into males and females and worker reproduction (reviewed in Ratnieks et al. 2006). Conflict over sex allocation may lead to a tug-of-war between queens and workers, in which each party attempts to bias the colony sex-ratio towards its optimum (Reuter & Keller 2001, Reuter et al. 2004, Pen & Taylor 2005). For example, workers may bias the sex-ratio by killing males (e.g. Sundström et al. 1996) or increase the proportion of diploid individuals raised as reproductive females (e.g. Hammond et al. 2002). Queens, in return, may limit the number of available eggs to prevent workers from eliminating males (e.g. Passera et al. 2001). These mechanisms of sex-ratio manipulation by queens and workers are likely to incur costs because of sub-optimal investment in workers and/or waste of resources already invested in the males eliminated (Reuter et al. 2004, Helms et al. 2005). Theory also suggests that female larvae are in conflict with both queens and workers, regarding their caste fate, and when in control of their development, a high proportion of female larvae should develop into reproductive females instead of sterile workers (Bourke & Ratnieks 1999, Reuter & Keller 2001, Ratnieks 2001, Wenseleers et al. 2003).

Because within-colony conflicts can decrease the number of active workers within a colony and change the ratios of worker castes when different types of workers vary in their likelihood to reproduce (Bourke & Franks 1995), these conflicts may reduce the evolutionary attainability and stability of division of labor. Thus far, models integrating self-organization and evolution have not dealt with selection at multiple levels; this is a point to address in future work.

Challenges

We end this review with a brief discussion of three aspects of models for the evolution of division of labor that we find particularly challenging.

Fitness

Empirically, little is known about how division of labor affects colony fitness. The relationship between ergonomic efficiency and fitness was one of the basic open questions pointed out by Oster and Wilson in their book *Caste and Ecology in the Social Insects* (1978). Thirty years later, little progress has been made. Current models use proxies for fitness, such as the overall work performed and the distribution of workers over tasks. Although these features are undoubtedly related to colony survival, growth and productivity, they do not necessarily have a simple and straightforward relationship with colony fitness. In fact, predictions based on such components of fitness (rather than on overall fitness) can be highly misleading (e.g. McNamara & Weissing 2010)). In the context of division of labor, it remains a challenge to develop more realistic approximations of the relationship between fitness and task performance, such as the number of reproductive individuals produced by a colony, as well as their reproductive values.

Realism of biological details

In the vast majority of models of division of labor, information on task needs is global. However, owing to the spatial distribution of tasks all group members are unlikely to have the same information. In a more realistic setting, group members should transmit information with some noise and cost.

Importantly, concerning the realism of evolutionary parameters, scientists working on self-organized processes at the colony level or evolutionary processes over many generations frequently have different backgrounds (e.g., mathematics, physics, computer science and engineering for self-organization models and evolutionary biology for ultimate questions) and hence use different approaches. For example, Tarapore et al. (2009) and Duarte et al. (in press, Chapter 3 of this thesis) use a high mutation rate, strong selection and few generations to minimize computation time. These authors follow the example of artificial intelligence studies, in which the goal is to develop fast solutions for highly complex systems in which several dynamic processes co-occur. From the engineering perspective of such studies, it makes sense to set parameters such as mutation rates or recombination probabilities to values that enhance the efficiency of the evolutionary algorithms. In contrast, evolutionary biologists are facing systems with externally given parameters, which may have less desirable properties. It remains to be seen how strongly evolutionary conclusions are dependent on the parameter settings used in simulations.

Comparison of division of labor in different models

Thus far we have treated division of labor as a concept that overlaps with specialization. However, it is desirable to distinguish between individual specialization, which is a property of the individual, and division of labor, which is a property of the group (Gorelick et al. 2004). To better compare different models, a standardization of the measures used for quantifying specialization and division of labor would be desirable.

Specialization has been quantified as the frequency of task performance by estimating the proportion of time individuals do specific tasks (e.g. Bonabeau et al. 1996). This measure, however, does not take into account the pattern of task choice. An individual switching randomly between two tasks and another switching only once during the observed period can achieve the same value of task frequency: They both spend half their time doing one task and the other half doing the other task. Another measure of specialization that is based on the probability of individuals to switch among tasks (Gautrais et al. 2002) produces a much higher value of specialization for the individual that switched tasks only once than for the individual that switched randomly between tasks.

Individual specialization is only part of the story, because we can talk about division of labor only if individuals are specialized in different tasks. Gorelick & Bertram (2007) suggested several matrix statistics, taking into consideration information on both tasks and individuals, which are useful measures of the nestedness of task choice (i.e., how restricted certain individuals are to certain tasks and vice versa). These statistics, however, do not account for the distribution of workers over tasks. To cope with the fact that each measure on its own offers only an incomplete picture of a model's behavior, it is perhaps necessary to include different measures, including a description of specialization at the individual level, a nestedness measure of tasks and individuals, and an overall task performance ratio.

Conclusion

Unification of evolution and self-organization will certainly enlighten us on what kind of mechanisms can evolve. However, empirically, little is still known about individual differences in behavior within colonies and the proximate mechanisms underlying the propensity of an individual to engage in a given task. The main obstacle to opening this black box lies in the difficulty of tracking individuals within colonies and manipulating their environment. Fortunately, new studies using radio tagging and fiduciary markers have begun to provide insights on the factors affecting the behavior of individuals within colonies and how, in turn, this influences interactions at the colony level. The combination of such behavioral analyses with new genomic tools applicable to a wide range of social insects (Grozinger et al. 2007, Graff et al. 2007, Wurm et al. 2010, Smith et al. 2010) should provide insights in how genetic differences and social interactions interact to jointly affect individual behavior and patterns of division of labor at the colony level.

Self-organization models and evolutionary models are two sides of the same coin. On one hand, we must understand the behavioral rules on which self-organization is based; on the other hand, a full understanding of division of labor must encompass the evolutionary trajectories of such rules. We hope that this review encourages more studies including both perspectives in their research agendas.

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Chapter 3

Evolution of self-organized division of labor in a response threshold model

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Behavioral Ecology and Sociobiology, in press

Abstract

Division of labor in social insects is determinant to their ecological success. Recent models emphasize that division of labor is an emergent property of the interactions among nestmates obeying to simple behavioral rules. However, the role of evolution in shaping these rules has been largely neglected. Here we investigate a model that integrates the perspectives of self-organization and evolution. Our point of departure is the response threshold model, where we allow thresholds to evolve. We ask whether the thresholds will evolve to a state where division of labor emerges in a form that fits the needs of the colony. We find that division of labor can indeed evolve through the evolutionary branching of thresholds, leading to workers that differ in their tendency to take on a given task. However, the conditions under which division of labor evolves depend on the strength of selection on the two fitness components considered: amount of work performed and on worker distribution over tasks. When selection is strongest on the amount of work performed, division of labor evolves if switching tasks is costly. When selection is strongest on worker distribution, division of labor is less likely to evolve. Furthermore, we show that a biased distribution (like 3:1) of workers over tasks is not easily achievable by a threshold mechanism, even under strong selection. Contrary to expectation, multiple matings of colony foundresses impede the evolution of specialization. Overall, our model sheds light on the importance of considering the interaction between specific mechanisms and ecological requirements to better understand the evolutionary scenarios that lead to division of labor in complex systems.

Introduction

Division of labor can be understood as the partitioning of work among specialists in a system, leading to an overall higher performance of the system. The study of division of labor is relevant across several disciplines, such as economics, robotics and biology, having a central place in the understanding of social evolution.

In eusocial insects, such as ants, bees, wasps and termites, division of labor among workers in the non-reproductive caste is often considered to be determinant of their ecological success (Hölldobler & Wilson 1990). At any given time, a colony performs different tasks in parallel, with different workers or groups of workers performing these tasks. For a long time, the central question regarding division of labor in eusocial insects concerned how seemingly simple individuals (from a cognitive perspective) can coordinate to perform the necessary tasks in an efficient manner.

Workers of an insect colony are not likely to have a general overview of the state of the colony, nor does a central command exist that distributes workers among tasks. It has been suggested that workers must make choices based on local cues of different behavioral stimuli and information obtained from nestmates (Gordon 1996, Bonabeau et al. 1997, Page & Mitchell 1998). Task specialization and an adequate worker distribution over tasks are not controlled by a central agency, but emerge through self-organization from the interactions of workers with their environment and nestmates. Several models have explored various types of behavioral rules that can lead to self-organized division of labor (reviewed in Beshers & Fewell 2001, Johnson 2010). However, these models do not address the question how these rules could arise in the first place (Duarte et al. 2011, chapter 2 of this thesis). Due to the impact of division of labor on colony productivity, and hence fitness, one would expect that the behavioral rules underlying division of labor are targeted by natural selection to produce adequate colony-level responses (Page & Mitchell 1998). Self-organization models tend to neglect the link between division of labor and colony productivity. Contrastingly, models that explicitly analyse the adaptive value of division of labor (Wakano et al. 1998, Wahl 2002, Tannenbaum 2007), tend to neglect the behavioral mechanisms behind it, treating individual task specialization and task generalization as fixed behavioral strategies. There is an urgent need for integrating both approaches and to study the interplay between behavioral mechanisms and evolution (Bonabeau et al. 1997, Page & Mitchell 1998, McNamara & Houston 2009). Few models have attempted to do this (see Waibel et al. 2006, Tarapore et al. 2009). Moreover, these models have not focused specifically on the evolution of specialization and its relationship with colony fitness.

The integration of the perspectives of self-organization and evolution is straightforward to achieve by clearly distinguishing between the timescale of self-organization (within generations) and the timescale of evolution (between generations). Within generations, individuals have a genetic make-up that determines the behavioral rules to

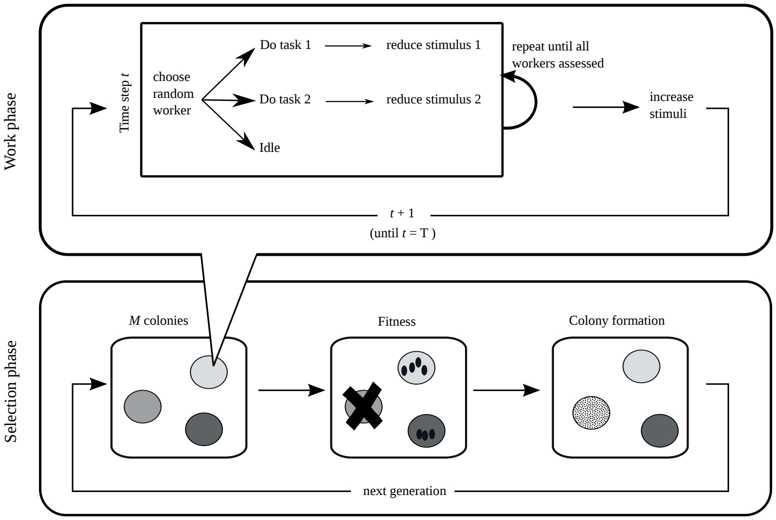

Figure 3.1: Schematic representation of the model, encompassing the time scale of self-organization ("work phase") and the time scale of evolution ("selection phase"). At the start of each generation, pairs of reproductive found colonies, each with workers. The colonies go through a work phase, where worker behavior is governed by the threshold model of division of labor: depending on whether task-specific stimuli are higher or lower than the genetically determined internal thresholds, workers will perform task 1, task 2, or do nothing. Each task-specific stimulus increases from one time step to the next, and it decrease again whenever a worker performs the task. After time steps, colony fitness is determined as a function of the amount work performed and its distribution over tasks. Colonies produce reproductives proportionally to their fitness, and these individuals found new colonies, which will enter a new work phase.

which they obey. Division of labor may emerge from the interaction between individuals. Depending on how well the emergent outcome fits colony needs, colonies will achieve lower or higher fitness, i.e., they will produce fewer or more reproductive individuals. Due to selection in the course of the generations, those behavioral rules that lead to adaptive division of labor will thrive (as illustrated by Figure 3.1).

In our study we consider the evolution of self-organized division of labor by introducing evolution in a well-known self-organization model, the response threshold model (Bonabeau et al. 1996, 1998). This model was chosen as point of departure because it has become a reference model for task choice among empiricists (e.g., Detrain & Pasteels 1991, Page et al. 1998, O'Donnell & Foster 2001, Weidenmüller 2004, Robinson et al. 2009a). The response threshold model assumes that individuals have inherent thresholds to respond to stimuli associated with specific tasks and, in a group, the individuals with the lowest threshold for a task will perform this task more often. An intuitive analogy in terms of human behavior is the sharing of house chores in humans: people with the lowest threshold for dish-washing, for example, will respond to the smallest accumulation of dishes, and will therefore do the dishes most of the times. Division of labor emerges from the differences between individuals in their thresholds.

Different versions of the response threshold model have looked at the effect of threshold reinforcement, colony size, number of tasks and genetic diversity (Theraulaz et al. 1998, Gautrais et al. 2002, Merkle & Middendorf 2004, Graham et al. 2006, Jeanson et al. 2007, Gove et al. 2009) on division of labor and colony performance. These studies assume that task stimuli are well-mixed in the environment; the cues used by individuals to choose tasks are therefore global. A recent article has explored the effect of spatial distribution of task stimulus on worker activity (Richardson et al. 2011) based on response thresholds; the results of this study suggest that a spatially explicit response threshold model, with local cues, shows similar behaviour as a non-spatially explicit model with global cues, at least when only one task is considered. Johnson (2010) showed that when considering multiple tasks, the spatial distribution of task stimuli can lead to short-term specialization, even in the absence of thresholds. We are interested in the evolution of long-term specialization, in which threshold distributions are thought to play a large role. We therefore focus on the simplest version of the response threshold model that allows for division of labor, considering only two tasks and fixed thresholds during worker lifetime (Bonabeau et al. 1996).

The initial model by Bonabeau and colleagues (1996) assumed from the start that there were two groups of individuals in a colony (referred to as castes), possessing different thresholds for the existing tasks. When differences are assumed *a priori* it is not surprising to find that individuals behave differently, and division of labor emerges. Our main goal is to investigate under which conditions consistent differences in individual thresholds may evolve from a homogeneous population and thus give rise to division of labor. We also test the ability of the response threshold model to generate an adaptive distribution of workers over tasks.

We largely follow previous work on the response threshold model when implementing the dynamics of task-associated signals. If the stimulus for a task is above the threshold value of an individual, the individual has a high probability to perform the task; otherwise the individual will be less likely to perform the task. Task stimuli decrease with work performed, making it less likely for individuals with higher thresholds to become engaged in the task later on. We start from homogeneous populations (where all individuals have identical thresholds) and allow parameters of the response threshold model to evolve, in order to investigate the conditions under which threshold differentiation (leading to division of labor) may evolve. In this context we also examine how multiple mating affects the evolution of thresholds and division of labor.

We focus on two aspects of division of labor: specialization, i.e., the probability that individuals stick to the same task, and work distribution, i.e., the proportion of workers performing the different tasks. Specialization may be adaptive for two reasons: first, specialists may become more efficient at their task, due to learning, training or gain of valuable information related to the task; second, specialization may allow the colony to avoid the costs of switching tasks (due to traveling time between task locations or cognitive costs) (Smith 1776). The distribution of workers over tasks is also crucial, since it should be adequate to the colony's needs (Gordon 1996).

Model structure

Within-colony dynamics

Individuals are assembled in M colonies with a fixed number N of workers (unless stated otherwise, $M=1000$ and $N=100$ in our simulations). Within-colony dynamics largely follows Bonabeau et al. (1996) (see sections A and B of the Supplementary material (SM)). Individuals possess a threshold for each of the two existing tasks (θ_i, $i=1,2$) that may differ among individuals and is fixed throughout the work phase. At T discrete time steps t ($0<t<T$, where $T=100$ in our simulations), we assess all individuals for task choice in a random order. Individuals perceive task-associated stimuli S_i with an error ε_i drawn from a normal distribution of mean 0 and standard deviation $\sigma=1$. For a given task, the individual is willing to perform the task if the perceived stimulus is larger or equal to the threshold. Otherwise, the individual will not perform the task. This is summarized by the function:

$$\phi\left(S_i,\theta_i,\varepsilon_i\right)=\begin{cases}1, & \text{if} \quad S_i+\varepsilon_i\geq\theta_i \\ 0, & \text{if} \quad S_i+\varepsilon_i<\theta_i\end{cases}. \tag{3.1}$$

Individuals not motivated to perform any task will stay idle. Individuals motivated to perform one of the tasks will work on the task (Figure 3.1). If individuals are motivated to do both tasks, they will perform one of the tasks at random. We assume that when an individual works on a task, the corresponding stimulus is immediately reduced (see below). Hence, different individuals may perceive different levels of stimulus for two reasons: the error (or noise) in stimulus perception and the order in which stimuli are assessed.

In line with the Bonabeau et al. (Bonabeau et al. 1996) model, stimuli change in time as follows: there is a constant increase δ with every time step and a decrease of α_i with every active worker, where α_i is the efficiency of work (how many work units an individual can do per time step). The stimulus dynamics is therefore described by the equation:

$$S_i\left(t+1\right)=S_i\left(t\right)+\delta_i-\alpha_i A_i\left(t\right), \tag{3.2}$$

where $A_i\left(t\right)$ is the number of workers active with task i at time step t. In our simulations, δ_i and α_i have the same values for all individuals and tasks ($\delta=1$ and $\alpha=0.03$), unless indicated otherwise. These values were chosen because preliminary simulations indicated that these values required the engagement of a majority of workers but were still well within the work capacity of the colonies. The chosen values are also equivalent to the values of stimulus increase used in Bonabeau et al. (1996), thereby rendering comparisons between the models easier.

Stimulus values have a lower boundary at zero; if reduced below zero by a worker, the stimulus is reset immediately to zero. There is no upper boundary to the stimulus level.

Fitness

For the evolutionary analysis, we considered two scenarios on how colony fitness depends on the work performed. In each scenario, we make assumptions on how colony productivity $w(t)$ at time step t might depend on the work performed on tasks 1 and 2 (A_1 and A_2, respectively). Subsequently, we assume that colony fitness W is proportional to the geometric mean of these productivity values over time (neglecting the first 10 time steps, to avoid initialization effects).

In our standard scenario, we assume that the productivity at a given time unit is given by the weighted geometric mean of A_1 and A_2:

$$w(t)=[A_1(t)]^{\beta} \cdot [A_2(t)]^{1-\beta}=A(t) \cdot p_1(t)^{\beta} \cdot p_2(t)^{1-\beta}, \tag{3.3}$$

where $A=A_1+A_2$ is the total number of acts performed for both tasks and $p_i=A_i/A$ is the proportion of work devoted to task i. The exponent β is a weighing factor indicating the relative importance of tasks 1 and 2, with $0<\beta<1$. If $\beta=1/2$, then both tasks are of the same importance; if $\beta=3/4$, the optimal work distribution is 3:1, with task 1 being performed three times more than task 2. Considering different values of allows us to test the ability of colonies to achieve different adaptive worker distributions. The multiplication of different components forces colonies to work for both tasks; working for only one task results in zero fitness.

As we will see, the above scenario puts much emphasis on the total amount of work done, downplaying the distribution over tasks. To correct for this, we considered another scenario. We changed eq. (3.3) by strongly accentuating the effect of the work proportion p_1:

$$w(t)=A(t) \cdot \exp\left[\frac{(p_1(t)-\beta)^2}{2\sigma^2}\right]. \tag{3.4}$$

The second term in eq. (3.4) is a Gaussian with maximum in that drops rapidly to zero if the 'standard deviation' σ is small (in our simulations, $\sigma=0.1$).

To start a new generation each colony produces a number of reproductives proportional to the colony's fitness. M pairs of reproductives are drawn at random from the offspring pool to form the new colonies. In the version of the model where colony foundresses are multiply-mated (polyandry), M foundresses are first chosen at random; for each foundress, m mates are then chosen at random. We also considered the situation where both parents mated multiply (polygynandry), but since the results did not differ from polyandry they will not be presented here. Ten replicate simulations of every parameter combination were run for each model, for 40,000 generations.

Inheritance

New individuals in a colony originate from the mating of the two parents of the colony, or from the mating of the colony foundress with one of m males, in the case of multiple mating. Offspring production occurs at two moments: a fixed number of N workers are produced before the start of the working phase, and reproductive offspring is produced at the end of the working phase. In case of multiple matings, paternity is equally shared among males; for each offspring, the father is chosen at random from the males with which the female has mated.

For simplicity, all individuals are haploid and genetically characterized by two genes, encoding the two task thresholds as real numbers, $\theta_1 > 0$ and $\theta_2 > 0$. When a new individual is produced, with probability r (the recombination rate) it inherits one threshold from the mother and the other threshold from the father. With probability $1 - r$ the individual inherits both thresholds from the same parent. The recombination rate lies between zero, when the two thresholds are inherited as one gene, and $1/2$, when the thresholds segregate independently. For the simulations shown in the main text, $r = 1/2$. We show results for $r = 0$ in the section E of the SM.

Mutations occur with probability μ per gene whenever new offspring is formed. The mutation step size is drawn from a normal distribution of mean zero and standard deviation σ_μ. Thresholds must be equal or larger than zero; when a mutation causes thresholds to fall below zero, they are reset to zero. No upper limit is set to the value of thresholds. In order to speed up evolution we chose a high mutation probability ($\mu = 0.1$). This choice was compensated by the use of a relatively small mutation step size ($\sigma_\mu = 0.1$).

Specialization

When an individual starts a task, we determine whether this is the same or a different task than the one previously done. The probability q of performing the same task in two subsequent time steps is a measure of individual specialization. We average q over all workers in a colony, and normalize the mean $\bar{q}$ by dividing it by the probability that individuals would stay in the same task due to chance alone. This probability is given by $p_1^2 + p_2^2$, where p_1 and p_2 correspond to the colony's proportion of acts for task 1 and 2, respectively. Note that individuals that remained idle for the entire simulation are

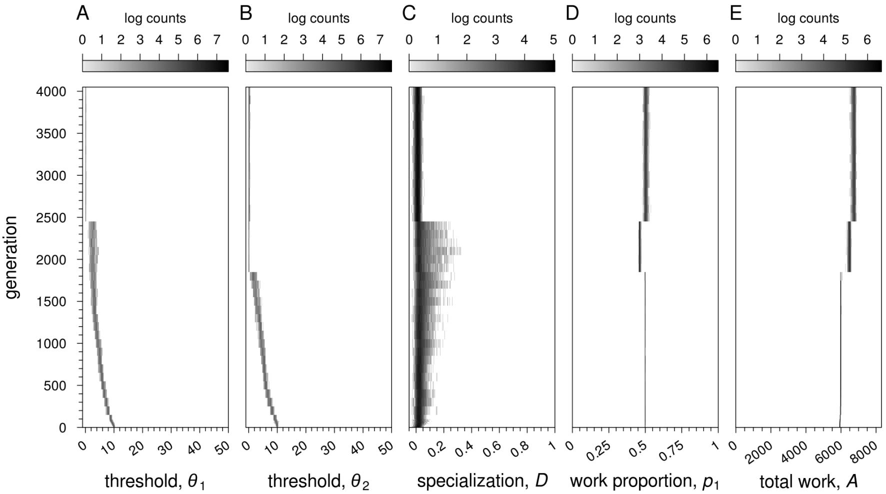

Figure 3.2: Evolutionary simulation of the response threshold model, for, under fitness scenario (3.3). Frequency distributions of thresholds (panels A and B), specialization (panel C), work proportion (panel D), and the total amount of work performed (panel E) over evolutionary time are shown. Thresholds for both tasks were initialized at 10 for all individuals. The graphs show the first 4000 generations. Grey scales on top indicate the frequency distribution of the trait depicted over M colonies (M=1000). Within about 2000 generations, the two thresholds θ_1 and θ_2 evolve to values close to zero (threshold values of each colony's parents are shown). Throughout the simulations, the proportion of work spent on task 1 (p_1, panel D), was close to 0.5, although a work distribution of $\hat{p}_1=\beta=0.75$ would have been optimal. Specialization first increased and later dropped to zero again. The total amount of work ($A=A_1+A_2$) increased over evolutionary time.

not taken into account for the calculation of $\bar{q}$. It can be shown that $0<\bar{q}/(p_1^2+p_2^2)\leq 2$. To obtain a standardized measure for the degree of mean worker specialization, we subtract 1 to obtain:

$$D=\frac{\bar{q}}{p_1^2+p_2^2}-1 \tag{3.5}$$

Hence, D varies from -1 to 1. For $D=0$, $\bar{q}=p_1^2+p_2^2$, implying that individuals choose tasks randomly. $D=1$ is achieved if all individuals fully specialize on one task, thus dividing labor. $D=-1$ indicates that individuals always switch between tasks from one time step to the next. In our simulations, D was always larger than or equal to zero.

Results

Evolution of thresholds and the work distribution

Figure 3.2 shows a representative simulation for the standard fitness scenario (3.3) and $\beta = 0.75$. All replicates showed essentially the same behavior. In less than 4000 generations, both thresholds evolved to zero levels (Figure 3.2AB). At first, a certain degree of specialization evolved in some colonies (D varying between 0 and 0.5), but specialization disappeared as soon as both thresholds reached zero (Figure 3.2C). Throughout evolutionary time, the evolved value of p_1 was always close to 0.5 (Figure 3.2D). Hence, both tasks were performed equally often, even though a value of $\hat{p}_1 = \beta = 0.75$ would have been optimal. In view of the drop in threshold values it is not surprising that the total amount A of work performed increased in the course of evolutionary time (Figure 3.2E).

In many other simulations (see below) we also found that selection in favor of a biased work distribution is not very efficient and that the work distribution tends to stay close to a value of $p_1 = 0.5$. To understand this, we took a closer look at the self-organization part of the model, namely at the stimulus dynamics (3.2). At equilibrium ($\Delta S_i = 0$), the number of workers for task i is:

$$\widehat{A}_i = \delta_i / \alpha_i. \tag{3.6}$$

Therefore, at stimulus equilibrium, the number of workers in each task depends solely on the stimulus parameters and not on the threshold values (see section B of the SM). As long as the values of δ_i and α_i are the same for all tasks (as in our simulations), $\widehat{A}_i$ will take the same value for all tasks i. Hence, any value of the thresholds should result in the same (unbiased) distribution of workers over tasks, given that stimulus equilibrium can be reached. Note, however, that the threshold values might affect whether and after how many time steps a stimulus equilibrium is reached in a simulation. These considerations are corroborated by (non-evolutionary) simulations of the work phase of the response threshold model (see Figure S3.6 of the SM).

The fact that the thresholds evolve to zero (Figure 3.2AB) is perhaps the most remarkable result of the simulations. Once the thresholds have disappeared, the whole threshold mechanism breaks down. Individuals are always motivated to perform any of the tasks, and individuals do not differ in their task preference.

In the simulations considered thus far, the thresholds presumable converged to zero because this maximizes the total amount work a colony can do. In fact, all individuals are busy all of the time when their thresholds are equal to zero. An obvious reason for this outcome might be the choice of fitness scenario (3.3), giving a high premium to an increase in A. For this reason, we also considered the alternative fitness scenario (3.4).

The evolutionary outcome changed when selection on a biased work distribution was made very strong, as in fitness scenario (3.4). Figure 3.3 shows the outcome for parameter values $\beta=0.75$ and $\sigma=0.1$. Now the threshold θ_1 for the "favored" task 1 still converged to zero, but the threshold for the other task, θ_2, exhibited evolutionary branching (Geritz et al. 1998) (Figure 3.3AB). In other words, a polymorphic population results where part of the population has θ_2-values close to 10, while the rest of the population has higher values that increase to values around 25. Due to branching, p_1 evolved to a higher value than 0.5, but still it remained at a considerably lower level than the optimal value (Figure 3.3D). Averaging across replicates, 33.8 ± 3.8 (mean±SD) of colonies show a high degree of specialization (D ranging between 0.5 and 0.7; Figure 3.3C). Specialization arises in those colonies where the parents differ in their values at the θ_2-locus (Figure S3.5 of the SM).

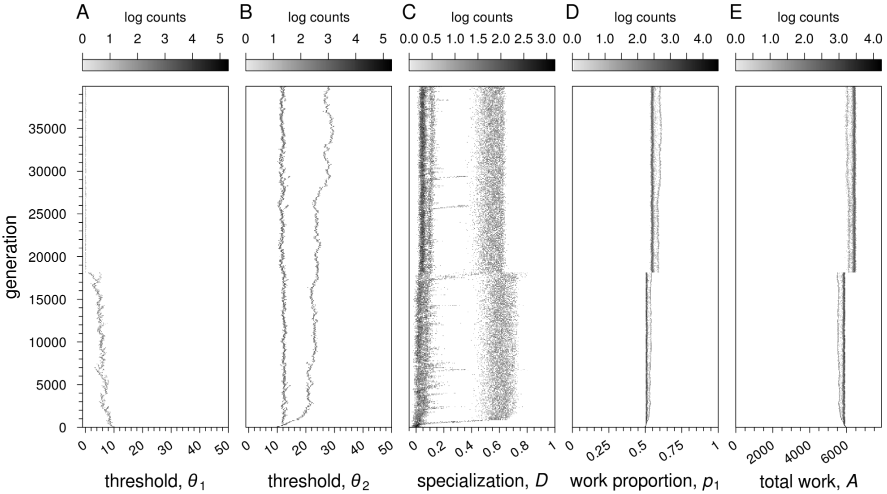

Figure 3.3: Evolutionary simulation of the response threshold model, for $\beta=0.75$, under fitness scenario (3.4) ($\sigma=0.1$). Graphical conventions follow Figure 3.2. $M=100$. θ_1 decreases to zero (panel A) and θ_2 branches (panel B). A proportion of colonies shows worker specialization, with D-values larger than 0.5 (panel C). Coinciding with the drop of to zero, work proportion, p_1 increases slightly but does not reach the optimal value of 0.75 (panel D). Total amount of work, A, also increases over evolutionary time (panel E).

Evolution of division of labor under these circumstances is a side-effect of selection on work ratio. Increasing thresholds leads to colonies achieving stimulus equilibrium later during the simulation; hence, overall, less work will be done for the task with the highest thresholds. Colonies which are polymorphic for θ_2 have an advantage because workers with $\theta_2=10$ will maintain the stimulus at a level between 15 and 20 (results not shown), hence below $\theta_2=25$. Consequently, in monomorphic colonies, fewer workers

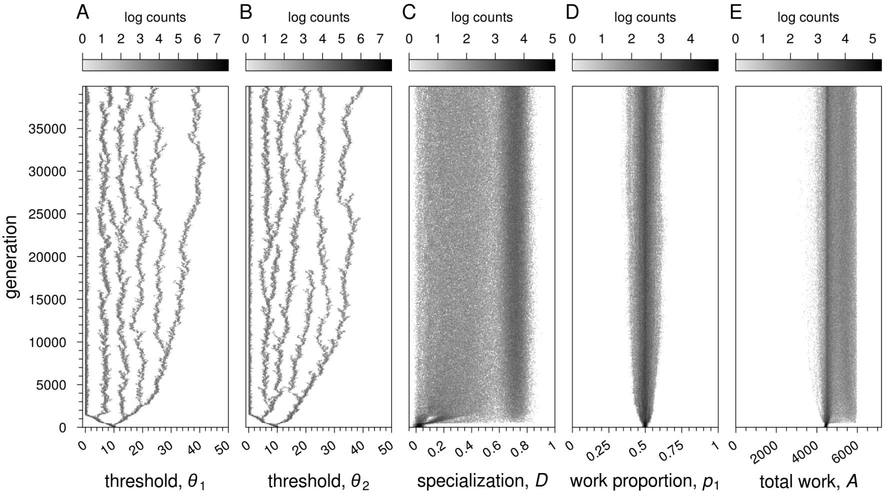

Figure 3.4: Evolutionary simulation of the response threshold model, when switching tasks is costly ($c=2$) and $\beta=0.5$, under the standard fitness scenario (3). The setup of the simulations and the graphical conventions are identical to Figure 3.2. Both thresholds diverged quickly into equally spaced multiple branches (panels A and B). Worker specialization increased quickly in the first 500 generations, with $55.6 \pm 2.8\%$ (mean±SD) of the colonies having a D-value larger than 0.5 (panel C). The work distribution varied among colonies around $p_1=0.5$ (panel D). In the first generations, colonies have perform a low amount ofwork (panel E), reflecting the fact that workers switching tasks have to stay idle for $c=2$ time periods. Part of the population recovers from this cost by evolving specialization.

are willing to perform task 2 than in polymorphic colonies.

Evolution of specialization

In the previous simulations specialization only evolved when a bimodal distribution of thresholds evolved due to evolutionary branching (as in Figure 3.3B). This indicates that the distribution of thresholds is key to the emergence of specialization. Indeed, a bimodal distribution of thresholds is assumed from the start in the self-organization model of Bonabeau et al. (1996). This model considers two “castes” of workers (“majors” and “minors”) such that $\theta_1^{majors} > \theta_1^{minors}$ and $\theta_2^{majors} < \theta_2^{minors}$. Not too surprisingly, the minors specialize on task 1, while the majors specialize on task 2. We obtained the same result under less constrictive conditions when initializing a population by drawing individual thresholds from two bivariate normal distributions (Figure S3.6B in the SM). As in the model of Bonabeau et al. (1996), task specialization converged to the maximal level $D=1$.

The question therefore arises when such a distribution of thresholds can evolve from scratch, starting from a homogeneous population. In Figure 3.3, the diversification of threshold θ_2 was driven by strong selection for a biased work distribution. To exclude this effect, we will from now on assume $\beta=0.5$. Moreover, we will mainly focus on our standard fitness scenario (3.3); in the SM we briefly present the results for fitness scenario (3.4).

In order to investigate whether evolution can shape colonies with a high degree of task specialization, we consider a scenario where worker specialization has a direct positive effect on colony fitness. To this end, we assume that switching between tasks is costly in terms of time, as proposed, as proposed by Adam Smith (1776). This is a simple, mechanistic cost that may result from the fact that tasks in a nest are spatially distributed (Sendova-Franks & Franks 1995), without having to make assumptions on the cognitive aspects of task performance. In our model, the switching cost is a time delay: individuals switching tasks must wait c time steps before engaging in the new task. We investigated values of c ranging from 1 to 8 time steps. Evolution of worker specialization occurred for $c\geq 2$, in a highly consistent way across replicates. In all replicate simulations, the increase in specialization was associated with multiple evolutionary branching of the two thresholds in the population. A typical simulation is shown in Figure 3.4. Some colonies achieved a high degree of specialization, but there was much variation in specialization across colonies (Figure 3.4C). This outcome was again highly consistent across simulations (Figure S3.12A of the SM). Averaging across replicate simulations, $55.6 \pm 2.8\%$ (mean±SD) of the colonies showed a value of at the end of 40,000 generations. As a result of specialization, individuals are able to avoid the cost of switching and the number of working periods increases (Figure 3.4E). Across colonies, there is a clear positive relationship between specialization and the number of working periods achieved (Figure S3.8, SM).

The level of specialization of the colonies depends on the thresholds possessed by the parents of the colony. When parental thresholds are similar for both tasks (i.e. $\theta_1^{mother}=\theta_1^{father}$ and $\theta_2^{mother}=\theta_2^{father}$), colonies show low mean specialization due to high similarity of thresholds among workers (Figure S3.9 of the SM). When parental thresholds differ for both tasks, colonies show higher mean specialization. Yet, notably, maximal specialization ($D=1$) is never reached, even when switching costs are very high (results not shown). This can be understood by considering an example: a colony where parental thresholds are $\theta_1^{mother}=\theta_2^{father}=10$ and $\theta_2^{mother}=\theta_1^{father}=40$. Owing to recombination, workers produced in this colony will fall into 4 types according to their thresholds: $\theta_1=\theta_2=10$; $\theta_1=\theta_2=40$; $\theta_1=10$ and $\theta_2=40$; $\theta_1=40$ and $\theta_2=10$. The first two types of workers will have no preference for either task, the third type will be more likely to perform task 1 and the fourth type will be more likely to perform task two. Hence, the mean level of specialization in the colony is decreased by the presence of workers of type 1 and 2.

The work distribution was also variable across colonies (Figure 4D), in a consistent way across simulations (Figure S3.12B, SM). Averaging across simulations, $73.3 \pm 2.2\%$ (mean$\pm$SD) of the colonies show a proportion of work for task 1 between 0.45 and 0.55 (Figure 3.4D).

Under strong selection on worker distribution (fitness scenario (3.4)), specialization typically did not evolve when $\beta=0.5$, for any of the switching costs tested (see Figure S3.13 of the SM).

Effect of multiple mating

It is often assumed that multiple mating of the queens has a beneficial effect on division of labor in social insect colonies (Oldroyd & Fewell 2007). To investigate whether this effect also occurs in the threshold model, we allowed foundresses to mate 2, 5, 10 or 15 times. As shown in Figure 3.5 the number of matings m does indeed have a strong effect on the evolution of specialization. Perhaps surprisingly, however, the evolved degree of specialization decreased with the number of matings. When females mated with 2 different males, the simulation results resemble those in the monogamy scenario considered in Section Evolution of specialization. However, fewer branches of the thresholds evolved within the runtime of a simulation (see example simulation in Figure S3.14 of the SM), and a lower proportion of colonies achieved $D>0.5$ (Figure 3.5A). When increasing the number of matings m, threshold branching and the associated evolution of specialization occurred in fewer and fewer simulations. For 5, 10 and 15 matings, the number of simulations in which the thresholds branched within 40,000 generations was 8, 5 and 2 out of 10 replicates, respectively.

Discussion

In our study we have analyzed the response threshold model (Bonabeau et al. 1996) from an evolutionary perspective. Previous work considered colonies with *a priori* differentiated castes, where it is not too surprising that division of labor will emerge. Our study shows that evolution, starting from fully undifferentiated, unspecialized workers, can lead to a state where differentiated workers divide labor in a self-organized manner. The trajectory to specialization involves evolutionary branching (Geritz et al. 1998) at the loci influencing task choice. Evolution of division of labor occurred when task-switching incurred costs to the colony, in terms of time that individuals had to spend inactive when transitioning between tasks. Interestingly, task specialization also evolved without direct benefits of specialization when task-related thresholds branched for other reasons (strong selection in favor of a biased distribution of workers over tasks).

Our results highlight an important drawback of the behavioral architecture encapsulated in the response threshold model. We have shown that, at stimulus equilibrium, the distribution of workers over tasks is not governed by the distribution of thresholds

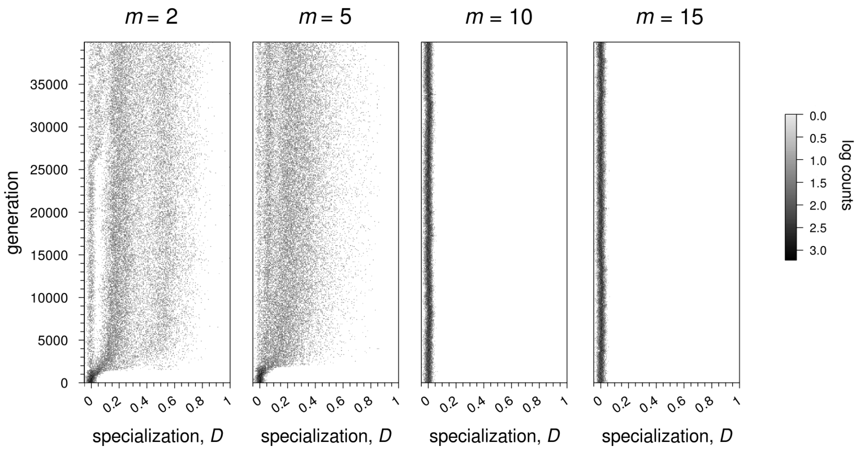

Figure 3.5: Evolution of worker specialization, D, in example simulations with different number of matings, *m*, under the standard fitness scenario (3.3). The evolved level of differentiation decreases with the number of matings.

in the population, but by the parameters of the stimulus dynamics. Even when selection on a particular distribution of workers over tasks is strong, the response threshold mechanism does not easily evolve a worker distribution that differs from the requirements imposed by the stimulus dynamics parameters. This constraint is relevant for the course and outcome of evolution. While it is easy to imagine how internal properties like thresholds could differentiate in the course of evolution, this is much less so for the properties of the stimulus dynamics. At least for tasks in which the stimulus corresponds to environmental cues such as temperature, humidity or food availability, the stimulus dynamics will be mainly externally imposed and hence, not subject to evolution. This general property of the threshold model indicates how the model could be put to the test experimentally. Our analysis leads to two specific empirical predictions. First, when placed under the same stimulus conditions, colonies with different distributions of thresholds should eventually produce the same distribution of workers over tasks. Second, when placed under different stimulus conditions, colonies with the same threshold distribution should, in a predictable manner, achieve different distributions of workers over tasks.

In our standard scenario, specialization only evolved under relatively high switching costs (i.e., when switching costs lead to a 25% or larger decrease in colony performance; Figure S3.7 of the SM). When costs were lower, the evolutionary tendency toward low thresholds was dominant, hampering evolutionary branching. In nature, the costs involved in switching tasks are most likely dependent on the tasks considered. It is plausible to consider that high costs, time-wise, are involved in switching between tasks like foraging and nursing, since the physical location of these tasks is far apart. Furthermore, to switch between such tasks, individuals may also "pay" physiological costs – for example, in the honey bee, the transition to foraging implies physiological changes which take some time to reverse (Huang & Robinson 1996). However, for other tasks which are closely located and/or physiologically independent, such as nursing and maintenance of nest temperature, it is not plausible to consider high switching costs and we would expect switching to occur more often between these tasks, as seen in middle-aged honey bees (Johnson 2003).

The main constraint on specialization in the current implementation of the threshold model is the need for non-random variation, where a part of the colony must have $\theta_1 \gg \theta_2$, and the other part $\theta_1 \ll \theta_2$. Note that here division of labor is an emergent property, since it results from the interaction of individuals with different combinations of thresholds. The fact that threshold values in the population evolve into multiple branches (i.e. the population is polymorphic for threshold values) decreases the probability that individuals inherit similar threshold values, thus helping in creating the diversity needed for specialization.

Such a constraint implies that the optimal colony phenotype is destroyed by recombination. In accordance with this argument, we observed higher values of specialization in simulations where thresholds evolved in complete linkage (see section E of the SM). Yet, even in the absence of recombination, a part of the colonies showed no specialization, owing to the pairing of individuals with non-complementary thresholds. In natural systems, the lack of division of labor resulting from unfavorable combinations of parents could be avoided through the evolution of disassortative mating. If mating would preferentially occur between reproductives with a complementary threshold, a much higher degree of task specialization within the colony would result. Unfortunately, little is known about mate choice in social insects and it seems that it is unlikely to be an important force in species such as ants and termites where males cannot mate multiply (Boomsma et al. 2005).

There is some evidence that multiple mating has beneficial effects on division of labor and colony productivity owing to genetic task determination (e.g., Mattila & Seeley 2007, Oldroyd & Fewell 2007). Improved colony performance and increased disease resistance due to high intra-colony genetic diversity are the two major explanations for the presence of multiple mating in several species of eusocial insects (Brown & Schmid-Hempel 2003). A few theoretical studies, based on the response threshold model, have supported the hypothesis that multiple mating does have beneficial effects on colony performance (Graham et al. 2006, Gove et al. 2009, Tarapore et al. 2009). In view of this evidence, our finding that increased number of matings did not facilitate the evolution of specialization is surprising. A possible explanation is that mutations in threshold values do not have as strong an effect on colony fitness if the foundress is multiply-mated. Under single-mating, a male and female with thresholds varying in the opposite direction (i.e., at the extremes of the threshold distribution), would produce a colony with considerably higher fitness, thus leading to a quick spread of the new alleles in the population. If the female is multiply-mated, parentage of workers will be shared equally among males (the majority of which not carrying the beneficial mutations) and only a small proportion of workers within the colony will possess the threshold combination leading to specialization. Our results suggest that multiple mating may only promote specialization if genetic diversity in task-choice alleles is already present. Our findings are also in line with previous work that showed that, in general, multiple mating decreases the variance in colony performance, and therefore is less beneficial when the average colony performance is poor (Rueppell et al. 2008). In our model, average colony performance can be considered poor when task switching is costly and colonies are monomorphic. These results once again illustrate how adding evolution to self-organization models may lead to different insights and conclusions.

Colony size has been argued to influence division of labor, with larger colonies having more specialized workers (Anderson & McShea 2001). Previous work on threshold models supports this argument (Gautrais et al. 2002, Merkle & Middendorf 2004, Jeanson et al. 2007). In our study, we focused on a colony size of 100 individuals, but we also considered colonies consisting of 20, 50, 500 and 1000 individuals. Colony size did not qualitatively affect the results obtained for any of the studied colony traits (see Figure S3.17 of the SM). The discrepancy between previous models and ours is likely owing to differences in the implementation of the stimulus dynamics and of the threshold mechanism itself. A more technical comparison of different threshold models would be useful to fully understand how colony size can influence division of labor under a threshold mechanism.

In evolutionary models of division of labor, choosing an adequate measure of colony productivity or fitness can be rather complex. In real social insects, the actual relationship between workload completed, ratio of work over tasks, and colony fitness is not well defined. Here we tested two functions which give emphasis to different fitness components. Using a fitness function that gives high priority to the distribution of workers over tasks produced different results than our standard fitness scenario. Even in the absence of switching costs, evolutionary branching of (one of the) thresholds and worker specialization evolved. However, even under these circumstances, the limitations of the threshold model remained and the optimal work ratio was not achieved. Interestingly, the same fitness scenario (eq. [3.4]) that induced task specialization in the absence of switching costs (for the case $\beta=0.75$, favoring a biased distribution of workers over tasks) prevented task specialization even in case of high switching costs when a 1:1 work distribution was optimal ($\beta=0.5$). This is likely because branching of thresholds introduces variation in the work distribution, and colonies that deviate from the optimal 1:1 work ratio are severely punished. Hence, in contrast to the other fitness function, the selective pressure on work distribution functions as an obstacle to the evolution of specialization. This illustrates that the simple architecture encapsulated in the threshold model cannot cope optimally with multiple selective pressures.

Several other avenues of research would be fruitful for future studies. One possibility is to consider more open behavioral architectures, for example using evolvable neural networks, where external stimuli are picked up and further processed by various layers of neurons, which eventually determine what kind of behavior results from the given input. Recent studies using neural networks indicate that a diversity of evolutionary outcomes is conceivable under a more open architecture, some of which are impossible in the fixed response threshold model, such as the possibility for the stimulus of one task to influence directly the behavioral output for another task (Lichocki et al. 2012, Duarte et al. 2012, chapter 5 of this thesis). Such an open architecture can overcome the constraint of the threshold model that only specific worker distributions over tasks are feasible.

Another avenue of research is to consider the role of phenotypic plasticity as a source of differentiation among workers. Here we consider behavior to be entirely determined by genetic factors, but in reality it has been found that developmental plasticity plays an important role in generating inter-individual variation (Oster & Wilson 1978, Robinson 1992, Weidenmüller et al. 2009). Likewise, experience has also been shown to have an effect on task choice in real colonies (Ravary et al. 2007). In an evolutionary version of the reinforced threshold model, where thresholds change after task performance, we observe that experience-based specialization overcomes the limitations imposed by recombination and random mating (chapter 4 of this thesis).

Our study is one of the first in a framework where complex adaptive systems are seen as the result of the interplay of natural selection and self-organization. More such studies are needed to help clarify the roles of these two forces in shaping such systems.

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Supplementary material

In this supplement, we provide additional information about our model and the dependence of the model behavior on the various model variants and model parameters. The supplement consists of the following six sections:

- A. Implementation of the response threshold model
- B. Stimulus and worker dynamics in the response threshold model
- C. Additional results for the model without switching costs
- D. Additional results for the model with switching costs
- E. Effect of recombination
- F. Effect of colony size

A. Implementation of the response threshold model

Our implementation of the response threshold model differs from the original model by Bonabeau et al. (1996) in a few aspects. First, we assume more explicitly than Bonabeau and colleagues that stimuli are perceived with noise (see section B). Second, in the original model individuals meet only one of the task stimuli (with equal probabilities); therefore there is never a situation where an individual is willing to do both tasks. Our tie-breaking mechanism in such situations (random choice between the two tasks) is nevertheless comparable to the original implementation. The third difference regards the update of the stimulus with every individual's action. This implies that individuals may perceive different stimuli, which does not occur in the original implementation. The fourth and last difference is that we waiver the assumption of the original model that, once they have chosen a task, individuals stick to this task for 5 time steps on average, regardless of stimuli values. Hence, at least in part, specialization is already built into Bonabeau et al.'s model. In our model, individuals assess task stimuli at every time step.

B. Stimulus and worker dynamics in the response threshold model

Bonabeau et al. (1996) assumed that – given a stimulus S_i and a threshold θ_i – an individual will perform the task with probability:

$$\Phi_i = \frac{S_i^n}{S_i^n + \theta_i^n}. \tag{S3.1}$$

For large values of the parameter n, the "responsiveness" comes close to the usual interpretation of a threshold process: $\Phi_i = 1$ if $S_i > \theta_i$ and otherwise $\Phi_i = 0$. For smaller values of n, Φ_i is an S-shaped function of (Figure S3.1a). The interpretation of (S3.1) is that there is always a probabilistic element in decision making.

In our model, we make this probabilistic element explicit, by assuming that stimuli are perceived with a certain error. The probability Φ_i that a given individual with threshold θ_i for task i is responsive to the stimulus value S_i, is the expected value of the

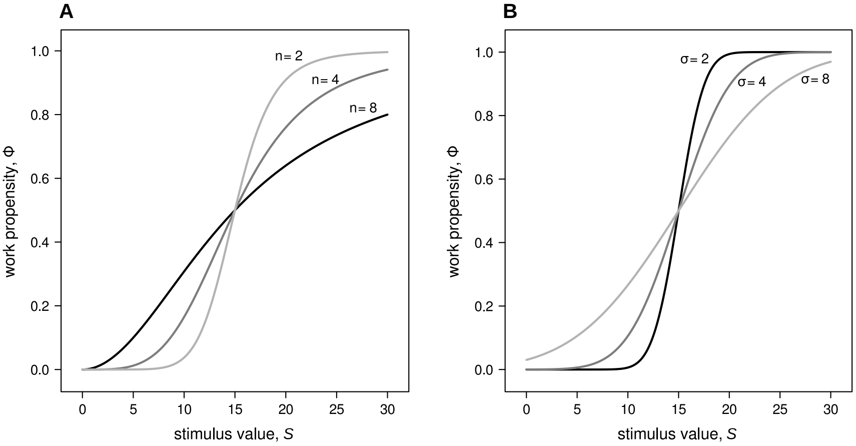

Figure S3.1: Probability of an individual with threshold $\theta_i = 15$ to be responsive to a given stimulus value in (A) the model of Bonabeau et al. (1996) and (B) our more mechanistic model.

function $\phi(S_i, \theta_i, \varepsilon_i)$, which is defined by eq. (3.1) in the main text. Φ_i corresponds to the probability that the normally distributed error term ε_i (with mean 0 and standard deviation) is larger than $\theta_i - S_i$. This probability can be written in the form:

$$\Phi_i = \frac{1}{2}\left[1 + \operatorname{erf}\left(\frac{S_i - \theta_i}{\sigma\ 2}\right)\right], \tag{S3.2}$$

where erf is the Gaussian error function (Abramowitz & Stegun 1972).

As for Bonabeau's function (S3.1), also in our model the propensity of individuals to engage in a task is increasing with the stimulus value in a sigmoidal fashion (Figure S3.1b). The steepness of the function in the vicinity of θ_i is increasing with the inverse of σ, while it is increasing with n in Bonabeau's model. Qualitatively the two approaches give similar results (Figure S3.1). Yet, our approach has a clear mechanistic underpinning which lacks in the original response threshold model.

We can now calculate the propensity of an individual with threshold θ_i to engage in task i at equilibrium. An individual will take on task i (rather than the alternative task j) under two conditions: either only task i is activated while task j is not (probability $\Phi_i[1-\Phi_j]$), or both tasks are activated (probability $\Phi_i\Phi_j$) and task i is chosen at random with probability ½. Accordingly, the expected number of workers engaged in task i is given by:

$$A_i = N(\Phi_i(1 - \Phi_j) + \frac{1}{2}\Phi_i\Phi_j. \tag{S3.3}$$

From eq. (3.6) in the main text we know that at equilibrium $\widehat{A}_1 = \widehat{A}_2 = \delta/\alpha$. Therefore, the propensities for individuals to engage in tasks at equilibrium are also the same ($\widehat{\Phi}_1 = \widehat{\Phi}_2 = \widehat{\Phi}$) and implicitly given by the equation:

$$N(\widehat{\Phi}(1-\widehat{\Phi}) + \frac{1}{2}\widehat{\Phi}^2) = \frac{\delta}{\alpha}. \tag{S3.4}$$

Solving this quadratic equation results in:

$$\widehat{\Phi} = 1 - \sqrt{1 - \frac{2\delta}{\alpha N}}. \tag{S3.5}$$

Hence, the propensity for a worker to engage in a task at stimulus equilibrium is only dependent on "external" parameters and not dependent on the thresholds of the worker.

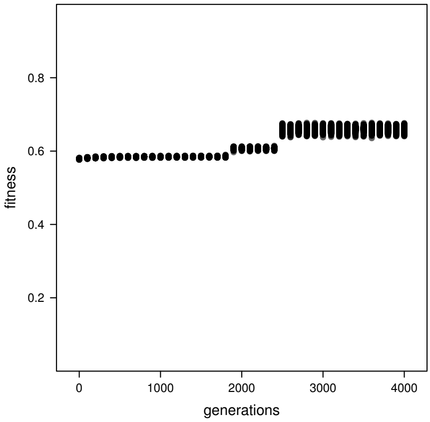

Figure S3.2: Relative fitness (i.e., fitness divided by the maximum possible fitness) for each colony in a simulation corresponding to Figure 3.2 ($\beta = 0.75$).

C. Additional results for the model without switching costs

For the simulations depicted in Figure 3.2 of the main text (where $\beta = 0.75$) the realized work distribution was close to 1:1, whereas a 3:1 ratio between tasks 1 and 2 would have been optimal. The thresholds evolved to values close to zero, most probably because this increases fitness by minimizing the number of idle individuals. Fitness values could, however, not achieve their maximum levels, due to the inability of colonies to reach the optimal work distribution (Figure S3.2).

When thresholds are close to zero, more workers are active than the number at stimulus equilibrium ($\widehat{A}_i = \delta_i/\alpha_i$) would suggest (Figure S3.3). This occurs because even at very low stimulus levels many workers will nevertheless be willing to perform the task due to errors in their perception. When thresholds are larger than zero, the equilibrium value of workers is well characterized by eq. (3.6). We corroborated the analytical result with simulations of the work phase of the response threshold model, without evolution of the thresholds. Simulations were run for colonies with normally distributed thresholds for the two tasks around means ranging from 5 to 30 and standard deviation 1. The ratio δ/α for task 1 was systematically varied, while keeping δ/α for task 2 fixed (δ_1/α_1 ranged from 10 to 50 and δ_2/α_2 was kept at 10). As expected, the ratio of work done for task 1 and work done for task 2 ($\widehat{A}_1/\widehat{A}_2$) at stimulus equilibrium depended only on the ratio δ_1/α_1, and not on the threshold values (Figure S3.4).

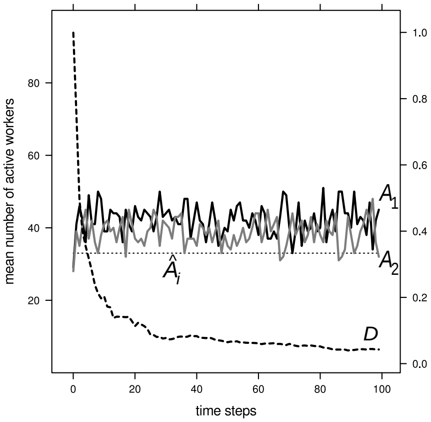

Figure S3.3: Worker dynamics in a colony where thresholds have evolved to values close to zero. The number of workers active on task 1 (solid black line) and task 2 (solid grey line) is considerably larger than $\hat{A}_i$ (dotted line). During the work phase, worker specialization drops to low values (dashed line)

In the simulations ran for fitness scenario (3.4), where there is strong selection on worker distribution, we found that, if a biased distribution was favored, evolutionary branching occurred in θ_2 and specialization evolved (see Figure 3.3 in main text). In Figure S5 we show the relationship between parental θ_2 and the level of specialization achieved by the colonies at the end of 40000 generations. Colonies whose parents differ markedly in show higher levels of specialization.

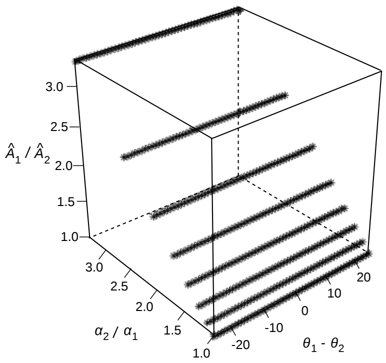

Figure S3.4: Ratio of workers for the two tasks at stimulus equilibrium is plotted against different ratios of work efficiency and differences between thresholds. Colonies were initialized from a normal distribution, with the same mean threshold and standard deviation 1. Mean threshold values were varied from 5 to 30, in steps of 1, and every combination was tested. Each point corresponds to the average of 10 simulations. The ratio of workers clearly changes with the ratio of the efficiency parameters, but is not affected by the mean difference between thresholds

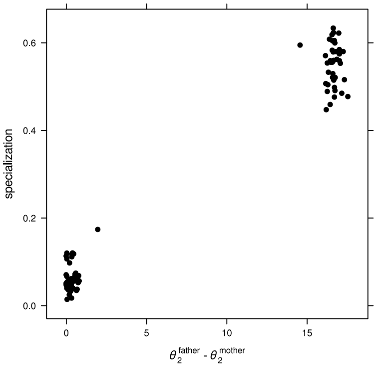

Figure S3.5: Mean worker specialization plotted against the absolute difference between the values of the branching threshold θ_2 of the colonies' parents. Each data point represents one colony ($M=100$) in a representative simulation, after 40,000 generations of selection under fitness scenario (4), $\beta=0.75$, $\sigma=0.1$

D. Additional results for the model with switching costs

First we ran simulations of the work phase of the threshold model to understand what threshold distributions could bring about specialization. Figure S3.6 shows a representative simulation for a case where the thresholds of all colony members are drawn from a unimodal distribution around an (arbitrary) mean for threshold 1 (here $\bar{\theta}_1 = 5$) and a unimodal distribution around a mean for threshold 2 (here $\bar{\theta}_2 = 20$). Irrespective of the considerable difference between threshold values, A_1 and A_2 converge to the same level, hence yielding an unbiased work distribution ($p_1 = 0.5$). Mean specialization is low, indicating that workers switch randomly between tasks.

When initializing a population by drawing individual thresholds from two bivariate normal distributions (Figure S3.6B), one with $\bar{\theta}_1 = 5$ and $\bar{\theta}_2 = 20$ and the other $\bar{\theta}_1 = 20$ and $\bar{\theta}_5 = 5$. As in the model of Bonabeau et al. (1996), task specialization converged to the maximal level ($D = 1$). A high degree of specialization can therefore be achieved if the thresholds in individual workers are negatively related to each other (as in Figure S3.6B).

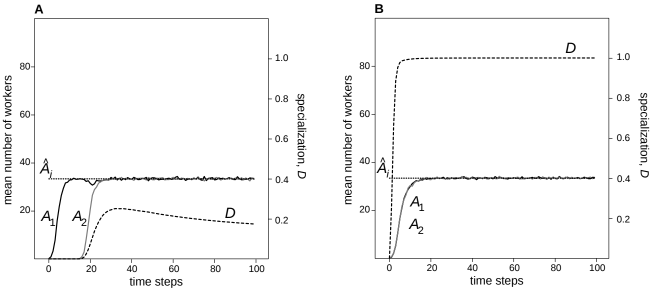

Figure S3.6: Distribution of workers over tasks and degree of specialization for a given distribution of thresholds in a colony. Both panels show the average of 100 colonies. In (A) the two thresholds of an individual were drawn independently from two normal distributions with $\bar{\theta}_1 = 5$ and $\bar{\theta}_2 = 20$ and standard deviation = 1. In (B) they were drawn from two bivariate normal distributions with a negative correlation -0.5: for half of the workers the bivariate normal distribution had means $\bar{\theta}_1 = 5$ and $\bar{\theta}_2 = 20$, while for the other half the distribution had means $\bar{\theta}_1 = 20$ and $\bar{\theta}_5 = 5$. In both panels, the number of active workers per task converge to the equilibrium value (eq. [3.6]; dotted line). In panel A), specialization (dashed line) only reaches a low level, while converges to the maximal value 1 in panel B)

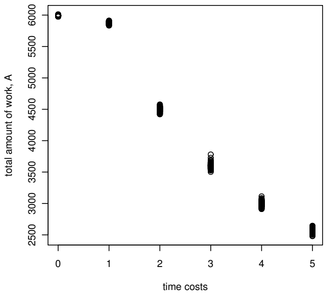

Figure S3.7: Effect of costs of task switching on the total amount of work performed. Six populations, with 100 colonies each, were simulated under different costs of task switching. Thresholds did not evolve but were randomly assigned to individuals, according to a normal distribution (mean = 5, sd = 1). For costs equal or higher than 2 time steps, the work performed in a colony is reduced by 25% or higher, respectively, compared to a population in the absence of switching costs.

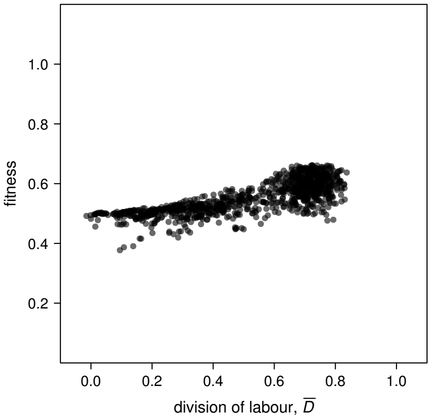

Figure S3.8: Relationship between the total amount of work performed in a colony and the degree of specialization within the colonies at generation $40,000$ ($c=2$).

In order to investigate if specialization could evolve from scratch in the response threshold model, we added a cost c to switching tasks, in the form of a delay in task performance whenever individuals choose to switch from their previous task. For costs equal to 2 time steps, the number of acts contributing for fitness decreased by one fourth (Figure S3.7). Evolution of specialization occurred through evolutionary branching of the thresholds, for $c \geq 2$. This was associated with an increase in work performed, which is brought back to values close to the work performed incolonies not suffering from switching costs, showing that specialized colonies are able to avoid switching and therefore spend more time working (Figure S3.8).

As expected, mean specialization was highest for colonies showing highly differentiated thresholds for both tasks. In Figure S3.9 we show the relationship between mean specialization obtained in colonies and the thresholds of colony parents, after 40,000 generations. Colonies where parental thresholds (for one task or both) are similar achieve little or no specialization.

At the end of each replicate simulation, we examined the behavior of the 10 colonies with highest resp. lowest degree of worker specialization, in order to understand what characterizes these colonies in terms of worker dynamics and threshold distribution. On average, colonies with a high degree of specialization have a larger number of active workers and reach the equilibrium number of workers of eq. (3.6) (Figure S3.10A).

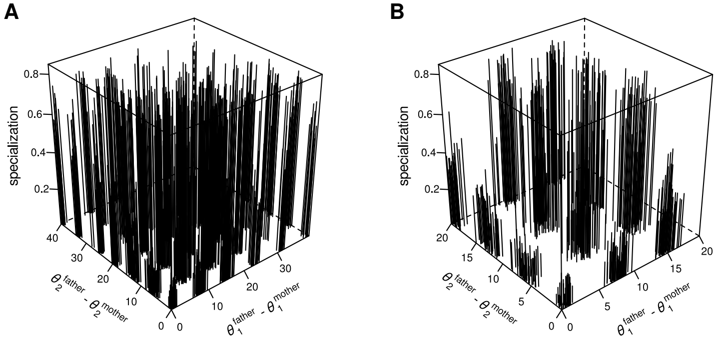

Figure S3.9: Relationship between colony specialization and the difference between parental thresholds for the two tasks. (A) Full data set of a typical simulation, after 40,000 generations. (B) To make effects more visible, the subset of colonies is shown where the difference between parental thresholds ranges between 0 and 20. Colonies whose parents show larger differences in both their thresholds typically have higher specialization values.

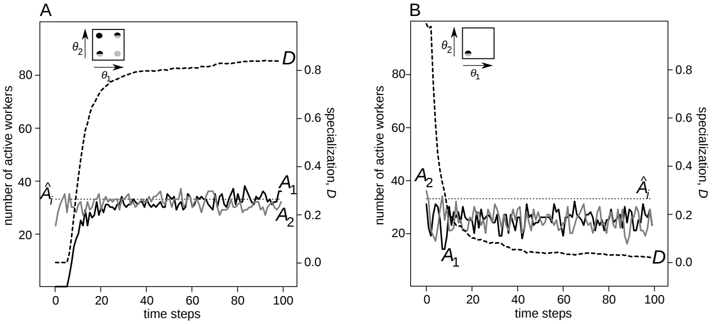

Figure S3.10: Worker dynamics of two extreme colonies from the last generation of the same simulation. (A) A colony with a high degree of specialization (hence, showing division of labor) and (B) a colony with a low degree of specialization (hence, no division of labor). On the left-hand *y*-axis, the number of active workers is shown, over simulation time steps (*x*-axis). The right-hand *y*-axis indicates the value of mean specialization in the colony (calculated as an average of the specialization values of all workers that are or were active). Insets in each graph illustrate the distribution of worker's thresholds. Each circle represents a group of workers with similar thresholds. Colors within the circles indicate the tasks performed by the workers (black for task 1 and grey for task 2)

Typically, colonies with high specialization have four types of workers, where the specialists have $\theta_1 \ll \theta_2$ or $\theta_1 \gg \theta_2$ and the other two types have very similar thresholds, either high or low (illustrated in insets of Figure S3.10A). Colonies without specialization do not show enough variation in thresholds to produce workers with different behavior (illustrated in inset of Figure S3.10B). These colonies also stay below the number of workers needed for stimulus equilibrium, due to the fact that workers spend time being idle, while switching between tasks. Figure S3.11 shows the frequency of worker performances for a typical colony with and without worker specialization. In the first case, a quarter of the individuals performs task 1 exclusively and at high frequency, while another quarter performs only task 2 exclusively and at high frequency (Figure S3.11A). A part of the individuals (approximately 30%) does not perform either task. As for the colonies without worker specialization, very few individuals perform one of the tasks exclusively (Figure S3.11B).

The results presented here and in the main text were highly repeatable across simulations. Figure S3.12 shows, for different simulations, the distribution of mean specialization and worker distribution over colonies.

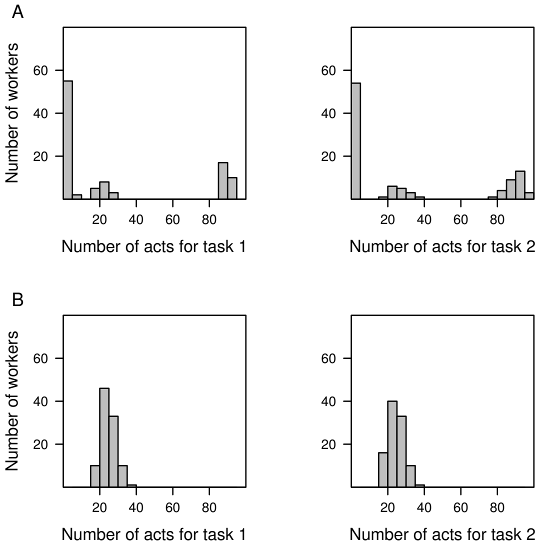

Figure S3.11: Histogram of worker performances for each task. Top graphs (A) correspond to the colony depicted in Figure S10A, where a high degree of worker specialization is observed. Bottom graphs (B) correspond to the colony depicted in Figure S10B, where worker specialization was very low

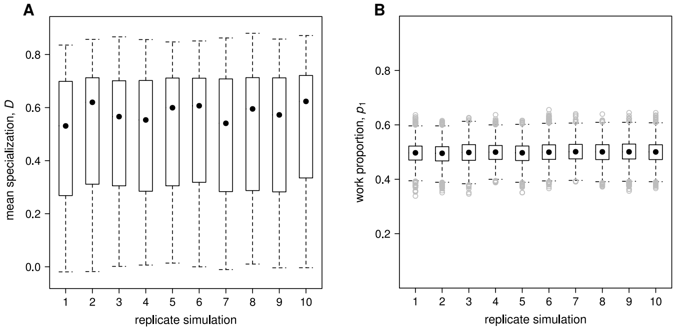

Figure S3.12: Distribution of (A) mean specialization, D, and (B) work proportion, p_1, across colonies that had evolved after 40,000 generations in different replicate simulations with $c=2$. All parameter values are as in Figure 3.2. Boxes show median (black closed circles) and interquartile range. Outliers are shown in grey open circles.

Strong selection on worker distribution

Under fitness scenario (3.4) it was not possible to evolve division of labor, when $\beta{=}0.5$. For low switching costs ($1{\leq}c{\leq}2$), the thresholds decreased to values near zero in all but one replicate, in which branching of the thresholds occurred. With increasing switching costs, threshold values did not drop to zero; in fact, for high switching costs ($c{\geq}4$), there was little change in thresholds throughout evolution (Figure S3.13). It is likely that these results are due to the strong selection for an unbiased work distribution. As observed in the previous simulations, when specialization evolves the variance of p_1 increases (for example, Figure 3.4D in main text), due to the diversification of thresholds. Under fitness scenario (3.4) any deviation from the optimal work distribution is severely punished, hence populations cannot evolve specialization.

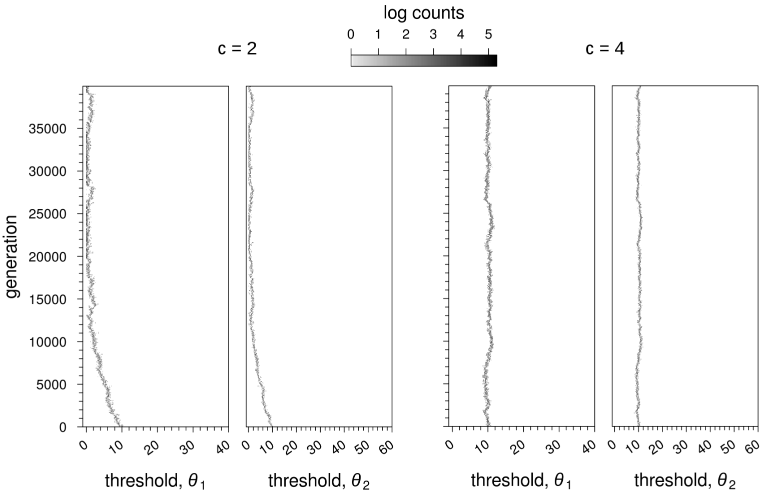

Figure S3.13: Evolutionary trajectories of thresholds in example simulations in which selection for worker distribution is strong (fitness scenario (4), $\beta{=}0.5,\sigma{=}0.1$). The presence of switching costs does not lead to branching of thresholds; with increasing switching costs, thresholds remain around their initial value of 10.

Multiple mating

The number of matings of female foundresses affected the evolutionary outcome under switching costs. When the number of matings, m, was low, specialization could evolve in all replicate simulations. However, the thresholds diversified into fewer branches (Figure S14); comparing Figure 3.4 in the main text and Figure S14, which differ only in m ($m{=}1$ and $m{=}2$, respectively), we also observe that the level of specialization obtained was lower when $m{=}2$, possibly because of lower differences between thresholds at the extreme of the distribution.

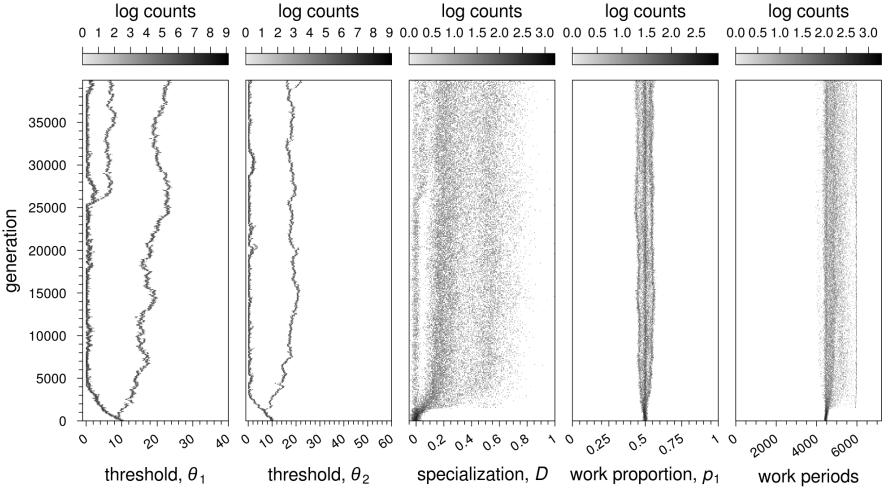

Figure S3.14: Evolutionary trajectories in example simulation with switching costs ($c=2$), and multiple mating ($m=2$), under the standard fitness scenario (3.3).

E. Effect of recombination

In the main text, we assumed that the thresholds are inherited independently from each other ($r=0.5$). It is conceivable that division of labor and worker specialization gets off the ground more easily if the thresholds are linked, allowing the coadaptation of the two thresholds. To check for this, we also considered lower values of the recombination rate r. Here we only present some results for the case of complete linkage ($r=1$), for the model with single-mating and the standard fitness scenario (3.3).

In line with expectations, specialization can evolve already for relatively small switching costs ($c \geq 1$, while $c \geq 2$ was required in case of $r=0.5$). Figure S3.15 shows a typical simulation with 1000 colonies. In contrast to the results in the main text, complete linkage allows maximal specialization ($D=1$) to be achieved by part of the population.

Linkage between the loci coding for the thresholds ($r=0$) enables the thresholds for the two tasks to evolve as a single locus. This facilitates the evolution of specialization. The divergence of the thresholds was associated with the evolution of a strong negative correlation between thresholds (Figure S3.16) – thus making it likely for individuals with a low threshold for one task to have a high threshold for the other task.

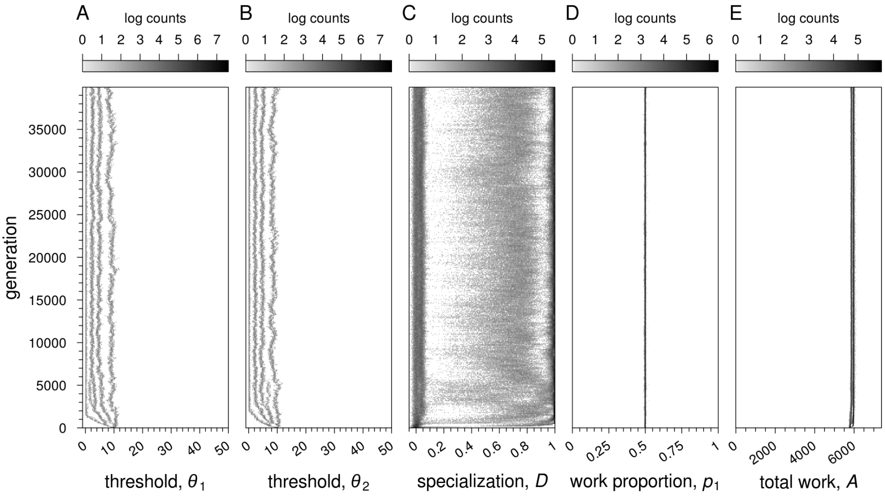

Figure S3.15: Evolutionary simulation of the response threshold model, for low switching costs ($c=1$) and complete linkage of the threshold loci ($r=0$).Graphical conventions, parameter values and fitness scenario as in Figure 3.4 of the main text.

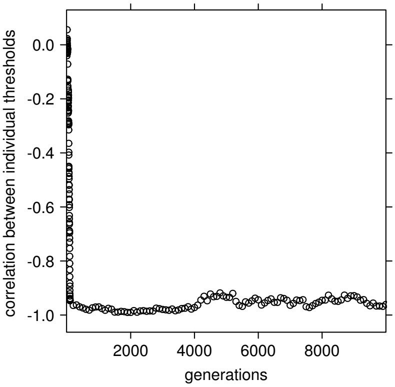

Figure S3.16: Correlation between individual thresholds in the simulation of Figure S15. The correlation becomes strongly negative, indicating that a high threshold for one task is associated with a low threshold for the other.

F. Effect of colony size

We investigated whether colony size N has an effect on the evolutionary outcome of our model, by running simulations for different N. Here we show the results for $N=20$, 50 and 500, under fitness scenario (3.3). The results show that colony size, in the current implementation of the response threshold model, does not affect the evolutionary outcome (Figure S3.17). There is also no qualitative difference between these simulations and the ones ran for $N=100$ (compare Figure S3.17A and S3.17B with Figs. 3.2 and 3.4 in the main text, respectively). We have therefore chosen to only show in the main text the results for $N=100$.

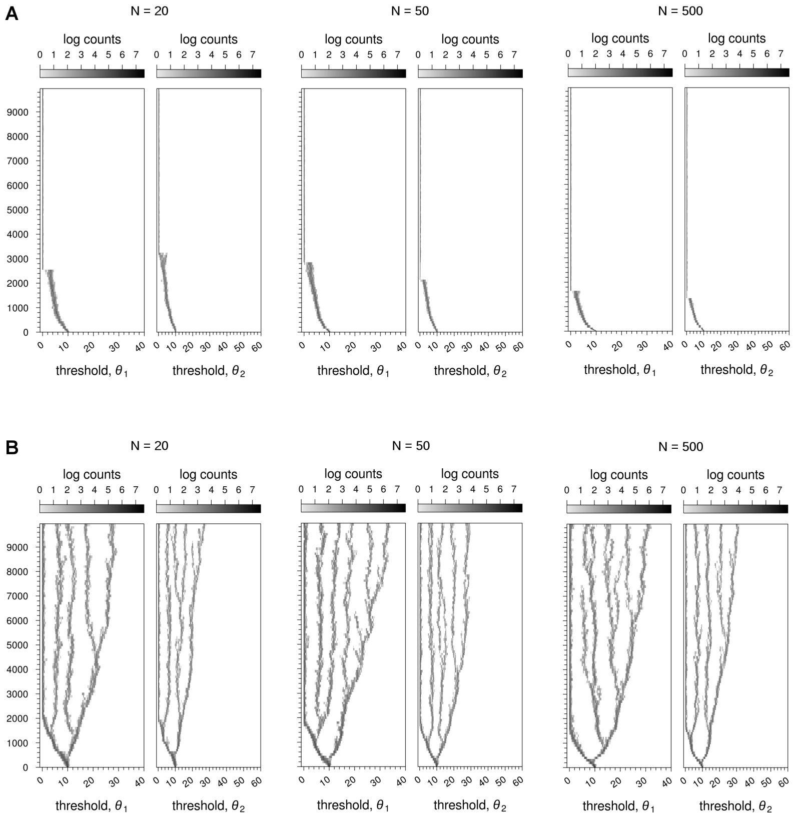

Figure S3.17: Evolutionary trajectories of thresholds for simulations with different colony size N (indicated above graphs). The simulations used the standard fitness scenario (3). (A) $\beta=0.75$ and $c=0$. (B) $\beta=0.5$ and $c=2$.

Chapter 4

Evolution of threshold reinforcement leading to division of labor

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Manuscript in preparation

Abstract

Threshold models for self-organized division of labor explain task specialization in insect societies on the basis of individual differences in response thresholds for task-specific stimuli. Individuals with a lower threshold for a given task have a higher propensity to perform this task than those with a higher threshold. According to the threshold reinforcement model, individual thresholds are not fixed, but change as a result of individual experience with a given task. Theoretical studies have shown that threshold reinforcement can explain the emergence of division of labor in an originally homogeneous population. However, neither the evolutionary origin of this mechanism nor its evolutionary stability has been addressed thus far. Here we allow for the evolution of the 'learning' and 'forgetting' parameter of the threshold reinforcement model. We investigate under what circumstances threshold reinforcement evolves from scratch, and when it leads to worker specialization. Interestingly, 'learning' (i.e. threshold reduction after the performance of a task) and, as a consequence, worker specialization did already evolve in a scenario where specialization did not have any fitness benefits at the colony level. In this scenario, evolved specialization is a by-product of selection in favour of threshold reduction. We also consider two scenarios with direct selection on specialization; either because switching between tasks is costly or because the efficiency of task performance increases with experience with this task. Not surprisingly, worker specialization could reach substantially higher levels than in the absence of selection for specialization. However, specialization could also drop to very low levels when the probability of gaining experience was considerably larger than the probability of losing experience. Our results demonstrate that details of the implementation of behavioral mechanisms can have major implications for the evolution of self-organized division of labor.

Introduction

Division of labor, the performance of different tasks by specialized individuals, is widespread in nature. Cooperation among individuals often involves a form of task specialization. For example, in species with biparental care, it is observed that the different sexes take on different roles, e.g., in hornbills (Kemp & Woodcock 1995) and cichlids (Itzkowitz et al. 2001). In social insects, the evolution of a sterile worker caste that performs the tasks essential to colony survival and growth, makes for one of the most striking examples of division of labor in nature (Oster & Wilson 1978, Hölldobler & Wilson 1990).

A typical social insect colony is composed of workers that perform different tasks related to the growth and maintenance of the colony, such as brood care, foraging, and nest defense. It has been proposed that behavioral differences among workers result from the existence of different response thresholds to task-associated stimuli, an idea formalized in the fixed response threshold model (Bonabeau et al. 1996, Page & Mitchell 1998). Stimuli can be, for example, the number of larvae present, or a signal of their level of hunger, the amount of food stored in the nest, temperature, or any other environmental cue that can be used as a proxy to perceive the need for a particular task. The basic idea of the fixed threshold model is that if a stimulus is larger than the corresponding threshold, the individual will perform the corresponding task. Individuals thus tend to perform more often those tasks for which they have lower thresholds. When there is variation in thresholds among individuals, division of labor may emerge in a self-organized manner.

Yet, it has been shown empirically that an individual's tendency to perform a task may change over time. There is much evidence that workers change tasks with age, for example (Wilson 1971, Oster & Wilson 1978, Wilson 1980, Seid & Traniello 2006). Ravary et al. (2007) observed that individual experience alone could generate specialization in different tasks and hence division of labor, in the ant *Cerapachys biroi*. Workers that had been exposed to successful foraging experiences were more likely to forage again than workers that had been exposed to unsuccessful foraging experiences, who in turn remained in the nest performing other tasks. *Cerapachys biroi* is thelytokous (workers are produced parthenogenetically by the queen) and has synchronous emergence of workers, meaning that a genetic and age effect can be eliminated. Workers also do not differ morphologically. In the ant *Camponotus rufipes* (Weidenmüller et al. 2009) and in bumble bees (O'Donnell & Foster 2001, Weidenmüller 2004), previous experience in certain tasks has been shown to increase the tendency to perform these tasks. A second potential effect of experience is on the performance efficiency of individuals. Johnson (1991) observed in seed-harvester ants that their handling efficiency of novel seeds increased with time. In *Temnothorax albipennis*, the presence of experienced individuals increases the speed at which colonies complete nest migration (Langridge et al. 2008). In *Camponotus rufipes*, workers become more effective at removing brood from high-temperature areas after previous experiences of similar situations (Weidenmüller et al. 2009).

A version of the fixed threshold model has been developed where thresholds change with experience. In this model, the successful performance of a task consequently lowers the corresponding threshold (Theraulaz et al. 1998, Gautrais et al. 2002), a process known as reinforcement. Threshold reinforcement can lead to differentiation of thresholds in an initially homogeneous colony. Owing to threshold differentiation, division of labor emerges. This model is the starting point for the present study.

While the reinforced threshold model is successful in obtaining individual specialization, it neglects the role of evolution in shaping the parameters for reinforcement, as do other self-organization models (see chapter 2 of this thesis). In previous work we have studied an evolutionary version of the fixed threshold model, which provided useful insights concerning the evolution of specialization and worker distribution (chapter 3). Similarly, here we will allow for the evolution of the parameters of a threshold reinforcement model.

In this theoretical study, we focus on the effect of experience on the tendency to perform a task and aim to identify circumstances that can lead to the evolution of experience- driven division of labor. We explore two scenarios that have been argued as reasons for division of labor to increase overall productivity by early economist Adam Smith (1776). In the first scenario we consider that task switching is costly, in terms of time. This simulates the cost that may come from tasks being located in different places. The second scenario considers a situation where the efficiency with which individuals perform a task increases with their experience in the task.

Model

The model is an extension of the fixed-threshold model considered in chapter 3 of this thesis (Duarte et al. in press). A population is composed of M colonies of N workers each (see Table 4.1 for parameter values). The model comprises a work phase, where workers must perform two tasks over T time steps, and a selection phase, where colonies obtain fitness based on the work performed during the work phase. In our study on the fixed-threshold model, the thresholds were genetically determined and subject to evolution. Now we study the evolution of the 'learning' and 'forgetting' parameters that determine the change of thresholds as a result of previous experience in the threshold reinforcement model.

Stimulus and worker dynamics

The dynamics of the work phase largely follow the assumptions of Bonabeau et al. (1996) and Theraulaz et al. (1998). There are two tasks to be performed, for a total of T time steps. In each time step, individuals, assessed in a random order, make a

Table 4.1: Parameters used in the two models, with and without experience-enhanced performance (EEP)

Parameter	Description	No EEP	EEP
M	number of colonies in a population	1000	1000
N	number of workers per colony	100	100
T	total time steps of work phase	1000	3000
α	work efficiency	0.03	–
$\alpha_{\max}$	maximum work efficiency	–	0.03
$\alpha_{\min}$	minimum work efficiency	–	3.3×10^{-5}
δ	stimulus increase	1	1
σ	standard deviation of noise in stimulus perception	1	1
μ	mutation probability	0.01	0.01
σ_μ	standard deviation of mutation step size	0.01	0.01
r	recombination probability	0.5	0.5
p_G	probability to gain experience points	–	0.2, 1
p_L	probability to lose experience points	–	0.2, 1

decision on what to do during the time step: perform task 1, perform task 2 or stay idle. Individuals decide what to do based on the perceived stimulus levels S_j, and their thresholds θ_j at the current time step. At the start of the time step stimulus levels increase by δ; whenever individual i performs a task j, the stimulus level of task j decreases by α_{ij}. In the baseline model, $\alpha_{ij}=\alpha_{\max}$ for all individuals (see Table 4.1 for parameter values), whereas in the model version where experience affects performance efficiency, α_{ij} depends on the experience of the individual with task j.

Individuals are motivated to perform a task if the stimulus level of the task, perceived with some noise, is above the threshold of this task (see chapter 3 for details). When individuals are motivated to do both tasks, one task is chosen at random to be performed. As explained above, the stimulus level is updated as soon as an individual decides to perform the task. As a consequence, during the same time step, individuals perceive different stimulus levels depending on how many workers have already chosen a specific task before them. Individuals are assessed every time step in a random order.

Threshold reinforcement

In line with Theraulaz et al. (1998) we introduce the 'learning' and 'forgetting' parameters λ and φ to model the feedback from individual experience to the threshold levels. When an individual performs a task j, its threshold θ_j is decreased by a value λ, which is a genetically encoded trait. If an individual does not perform a certain task, its threshold for that task will be increased by a value φ, also genetically encoded. Both λ and φ are initialized in our simulation at zero. All individuals start out with the same threshold values, thus the starting point of our model is identical to the fixed response threshold model of chapter 3. The reinforcement parameters λ and φ are allowed to evolve (see below).

Effect of worker specialization on colony fitness

Worker specialization was measured as in chapter 3, by calculating at the end of every generation the individual probability q of performing the same task in two subsequent time steps. We average q over all workers in the colony and normalize $\bar{q}$ dividing it by the probability of individuals staying in the same task due to chance alone. Mean worker specialization is then given by $D=(\bar{q}/p_1^2 + p_2^2)-1$, where p_1 and p_2 are the colony's proportion of acts for task 1 and 2, respectively. Subtracting 1 from the normalized measure of mean specialization allows us to obtain a value between -1 and 1. $D=1$ is obtained when workers never switch tasks; $D=0$ means that workers choose tasks randomly; and $D=-1$ indicates that workers switch tasks more often than expected by chance.

We consider three scenarios for the effect of worker specialization on colony fitness. In the first scenario, there is no direct selection on specialization. There is no cost to switching tasks, and all individuals are allowed to perform with maximal efficiency. In the second and third scenarios, we consider direct selection on worker specialization.

In the second scenario, there is a time cost to switching tasks. The implementation of switching costs follows chapter 3: if individuals choose to perform a task different than the previous one, they must wait for c time steps before being able to perform it. In this scenario, worker efficiency is fixed and equal for all workers (see Table 4.1).

In the third scenario, we assume that experience enhances performance efficiency (from hereon this model is called EEP). Individuals start with a minimum level of efficiency for each task j, $\alpha_{j\min}$. In this version of the model we also keep track of the individual level of experience e_{ij} for task j and we consider different probabilities for individuals to gain and lose experience. If task j is performed by individual i, e_{ij} is increased by 0.5 units with probability p_G. If task j is not performed during a time step by individual i, 0.5 units are subtracted from e_{ij} with probability p_L. With this implementation we can consider scenarios where the probability to retain experience may be different from the probability to lose it. Adding stochasticity to the model allows us to consider an effect of noise in the individual memory of past experiences. We tested four different combinations of p_G and p_L: p_G=0.2 and p_L=0.2; p_G=0.2 and p_L=1; p_G=1 and p_L=0.2; p_G=1 and p_L=1. Experience level affects efficiency following a logistic curve:

$$\alpha_{ij} = \alpha_{j\max} \frac{1}{1 + \exp(e_{ij})}, \tag{4.1}$$

where $\alpha_{j\max}$ and $\alpha_{j\min}$ are the maximal and minimal performance efficiency. See Table 4.1 for parameter values used in the simulations. For each combination of p_G and p_L we performed eight replicate simulations.

Selection and reproduction

Every time step, we record the work done on each task j, w_j, as the sum of the efficiencies α_{ij} of all individuals i performing this task. The first ten time steps of the simulation are not included in the calculation of fitness, to avoid initialization effects. At the end of the work phase, fitness, W, is calculated as the geometric mean of the work done for task 1 and 2:

$$W = \sqrt{w_1 w_2}\ . \tag{4.2}$$

Each colony then produces reproductive individuals in proportion to its fitness. Individuals are haploid and genetically characterized by two genes, which encode λ and φ. Individuals inherit these genes from the parents of the colony, with a mutation probability μ and mutation step size drawn from a normal distribution with mean zero and standard deviation σ_μ. Values of λ and φ are constrained to be positive, so if mutation reduces the values below zero, the allelic values are reset to zero. With probability r, recombination occurs and individuals may inherit each trait from a different parent. With probability $1 - r$, individuals inherit the two traits from the same parent.

New colonies are formed by a randomly mated pair of reproductives. The old colonies are replaced by the new colonies, and new workers are produced by the parents of each colony, following the same inheritance rules as the production of reproductive individuals.

Results

Baseline model: *c=0*, no EEP

In the absence of switching costs, 'learning' evolved to values substantially larger than zero in six out of the eight replicate simulations (λ=7.18 ± 1.05, mean ± SD across replicates). The 'forgetting' parameter remained close to zero in these simulations (φ= 0.01 ± 0.002, mean ± SD across replicates) (Figure 4.1A shows a typical simulation). Under this combination of 'learning' and 'forgetting', individuals tend to lower their thresholds if they perform a task, but not to increase them if they do not perform a task.

The evolution of learning to high levels brings an advantage to colonies because individuals quickly lower their thresholds to values near zero and thus engage in work at lower stimulus levels. This outcome is parallel to the evolution of thresholds to zero in the fixed threshold model (chapter 3). The mean work periods (i.e. on average, how many acts individuals perform in a colony, during a simulation) did increase slightly over the course of evolution (at generation 0, mean±SD across replicates was 666.4 ± 0.01; in the last generation it was 676.5 ± 3.63).

In the replicates evolving high 'learning', a relatively high level of mean worker specialization evolved (0.69 ± 0.003, mean ± SD across replicates), with little variation among colonies, after an initial period where 'learning' was low and worker specialization was highly variable (Figure 4.1A). Despite the high 'learning' evolved in the majority of simulations, mean specialization did not converge to the maximum level. Most individuals developed low thresholds for both tasks (Figure 4.2A), which means that they switched often between tasks. Some individuals, however, developed differentiated thresholds, thus becoming specialized in the task for which their threshold became lowest. The observed differentiation of thresholds is likely to be caused by initial differences between individuals in the stimulus levels perceived, owing to the fact that stimulus is immediately changed when individuals choose a task. Although the order of individuals is randomized in each time step, an individual that, by chance, in the first few time steps chooses the same task, reduces the threshold for this task, while increasing the threshold for the other. Hence, initial differences in stimulus perception have an impact in future time steps, leading to differentiation of thresholds in some of the individuals.

To confirm that threshold differentiation under high 'learning' only is caused by initial differences in stimulus perception, we ran non-evolutionary simulations for a range of 'learning' and 'forgetting' values, where stimulus is updated only at the end of each time step – hence all individuals perceive approximately the same level of stimulus. Indeed we observe that under this implementation specialization does not arise when only 'learning' is high (see Supplementary material (SM)).

Two replicate simulations differed from the majority, showing lower levels of 'learning' (0.52 ± 0.02, mean ± SD across the two replicates) and slightly higher levels of 'forgetting' (0.14 ± 0.03, mean ± SD) (see SM). Worker specialization in these simulations is quite variable among colonies, reaching values above 0.8 in some cases and low values on other cases. The evolutionary patterns of these simulations are very similar to the observed patterns in the initial generations of the simulations where 'learning' eventually evolved to high values. In these simulations, the time it took for 'learning' to evolve varied greatly among replicates. Therefore, it is possible that running the simulations for a longer time would produce the same end result: the evolution of 'learning' to high values and 'forgetting' to values close to zero. These results indicate that there must be a substantial difference between 'learning' and 'forgetting' for this to have an

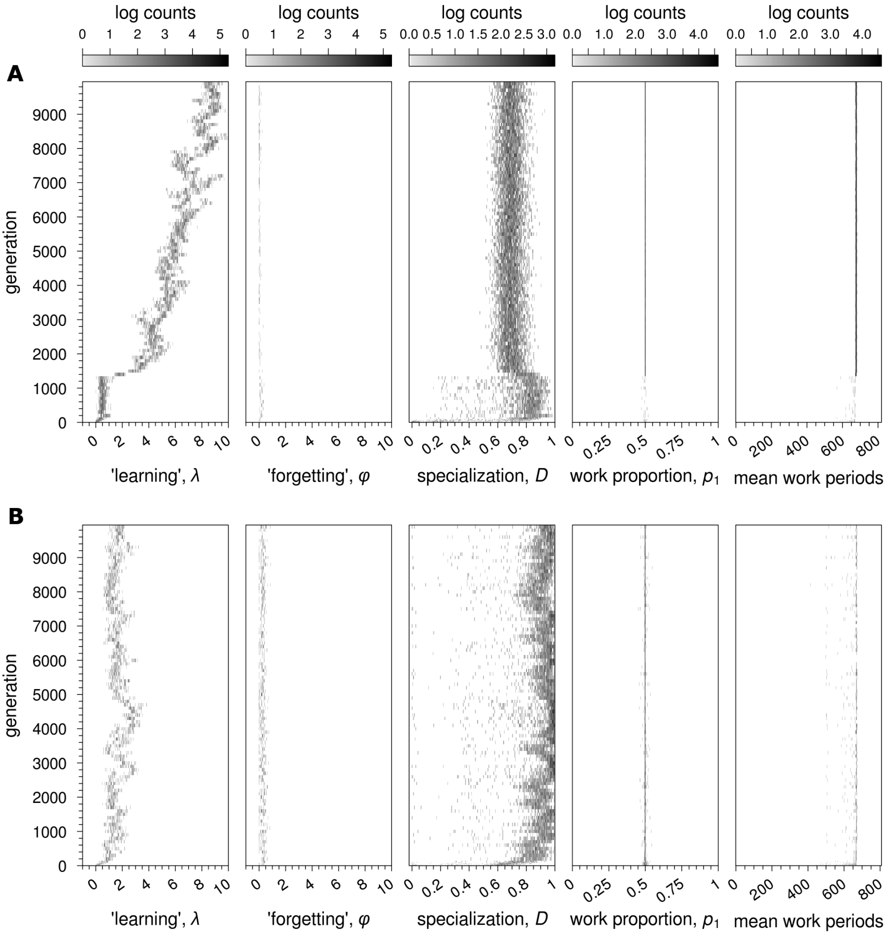

Figure 4.1: Representative evolutionary simulations of reinforced threshold model without experience-enhanced performance. Grey scales on top indicate the frequency distribution (log counts) of the trait depicted in each graph over colonies. (A) $c=0$. 'Learning' evolves to high values after approximately 1300 generations, whereas 'forgetting' remains close to zero. Mean worker specialization increases to relatively high values ($0.6<D<0.8$). (B) $c=2$. Both 'learning' and 'forgetting' evolve to values above zero, although 'forgetting' remains comparatively low (see main text for mean values). Worker specialization also evolves to values above 0.8.

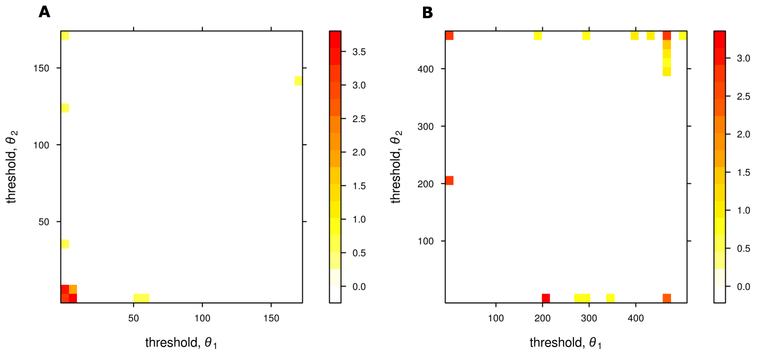

Figure 4.2: Frequency distribution of individuals' thresholds 1 and 2, for two representative colonies, at the end of the work phase (last generation). Color scale indicates the log count of individuals with the corresponding threshold combinations. (A) $c=0$, corresponding to the simulation in Figure 4.1A. Most individuals have low thresholds for both tasks, but a few develop differentiated thresholds, where one threshold is high and the other close to zero. (B) $c=2$, corresponding to simulation in Figure 4.1B. Individuals either develop differentiated thresholds or both thresholds become high.

effect in colony fitness. Hence, only when a high enough value of 'learning' appears in the population by mutation, can the evolution of 'learning' take off in the population. This indicates that stochasticity plays an important role in the outcome of this model.

Effect of switching costs

In the presence of switching costs ($c=2$), both 'learning' and 'forgetting' typically evolve values larger than zero (as in Figure 4.1B), although 'forgetting' (0.3 ± 0.06, mean ± SD across replicates) is lower than 'learning' (1.95 ± 0.95, mean ± SD across replicates). The majority of colonies ($90.34 \pm 5.3\%$ of colonies, mean ± SD across replicates) shows mean levels of worker specialization higher than 0.8. The evolved 'learning' and 'forgetting' parameters induced high differentiation in individual thresholds (representative colony in Figure 4.2B), which allowed for high levels of worker specialization. Results were similar for higher switching costs (see SM).

Experience-enhanced performance

In the model with EEP, three of the four parameter combinations of p_{G} and p_{L} tested yielded a similar outcome, while one combination differed markedly from the others (Table 4.2). For the majority of parameter combinations, 'forgetting' evolved to values above 1 and 'learning' remained at zero or very low values (Table 4.2, example simulation in Figure 4.3A). Despite the low 'learning' values, worker specialization arose in these simulations, reaching values above 0.8 for most colonies (Table 4.2). Mean work periods decreased in all cases, because worker specialization leads to an increase in efficiency in stimulus removal. Hence, individuals required fewer time steps to remove the same amount of stimulus.

For the parameter combination where p_{L} is markedly smaller than p_{G} , 'learning' evolves to values considerably larger than zero, whereas 'forgetting' remains close to zero (Table 4.2, example simulation in Figure 4.3B). Mean worker specialization remains at low values (Table 4.2, Figure 4.3B). However, the lack of worker specialization under this parameter combination does not result in lower fitness when compared to the simulations where specialization evolves (see Supplementary Material). This can be understood by examining the gain in worker efficiency in the two situations. Under the parameter combinations where only 'forgetting' evolves, workers develop maximal efficiency for one of the tasks (Figure 4.4A). Under the parameter combinations where 'learning' evolves, but not 'forgetting', worker efficiencies can increase to the maximum for both tasks (Figure 4.4B). In the former case, individuals avoid performing an unfamiliar task to minimize the risk of losing efficiency in the familiar task, whereas in the latter case, the probability to lose efficiency is small, even if individuals switch tasks often. Individuals can therefore switch tasks, reaping the benefits of increased efficiency in both tasks.

We have observed in the model without EEP that high levels of 'learning' can lead to relatively high levels of specialization, yet similar evolutionary trajectories of 'learning' do not lead to high specialization in the model with EEP. This difference occurs because, in the model with EEP, individuals start out with minimal efficiency in stimulus removal. Therefore, the task stimuli accumulate, motivating individuals to engage in the different tasks and gain experience in them. In the model without EEP, individuals start out with maximal efficiency in stimulus removal. Hence, individuals that have not performed a specific task in the first time steps are unlikely to perform it later on, because the stimulus for that task will have been removed already by other workers, who have consequently lower thresholds for that particular task.

Discussion

Here we have analysed the evolution of threshold reinforcement under different scenarios for the effect of worker specialization on colony fitness. Just as in the fixed threshold model, for specialization to occur, individuals in a colony must have different thresholds (see chapter 3). However, in the reinforced threshold model, differentiation of thresholds results from the positive or negative feedback caused by the 'learning' and 'forgetting' parameters.

The first scenario modelled did not consider direct selection on worker specialization. Yet, selection to minimize idleness led to increased worker specialization. In order to decrease worker idleness, the 'learning' parameter evolved, resulting in individuals lowering their thresholds after performance of a task, an outcome parallel to

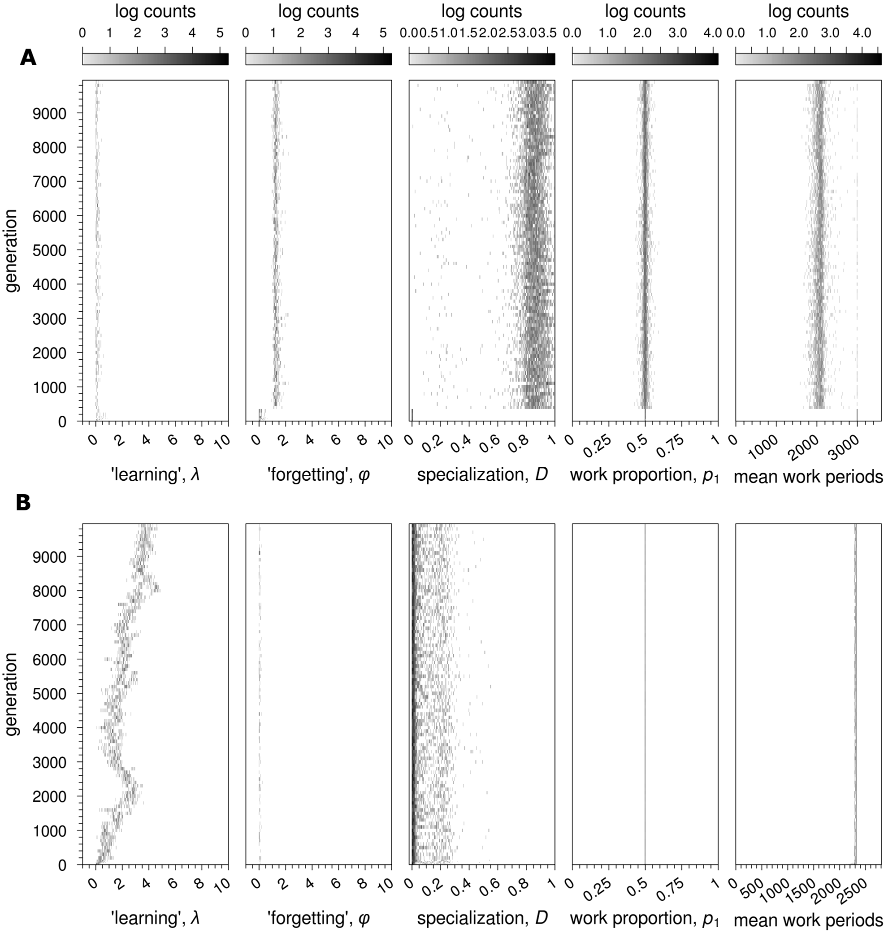

Figure 4.3: Representative evolutionary simulations of reinforced threshold model without experience-enhanced performance. Graphical conventions follow Figure 4.1. (A)$p_G = 1$, $p_L = 1$. 'Learning' remains around zero, whereas 'forgetting' evolves to values larger than zero (see Table 4.2 for means and standard deviations across replicates). Mean worker specialization increases to relatively high values ($0.6 < D < 0.8$). (B) $p_G = 1$, $p_L = 0.2$. 'Learning' evolves to large values, 'forgetting' remains around zero. Worker specialization remains low.

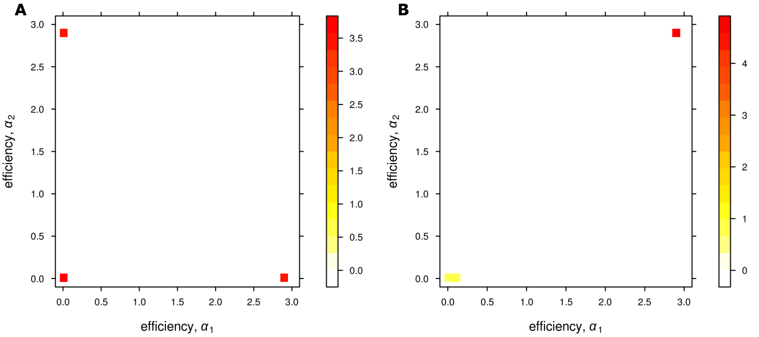

Figure 4.4: Frequency distribution of individuals' efficiencies for task 1 and 2, for two representative colonies, at the end of the work phase (last generation) of the experience- enhanced performance model. Graphical conventions follow Figure 4.2. (A)$p_G = 1$, $p_L = 1$ corresponding to the simulation in Figure 4.3A. Individuals have either high efficiency for one of the tasks, or low efficiency for both. (B) $p_G = 1$, $p_L = 0.2$, corresponding to simulation in Figure 4.3B. Most individuals develop high efficiency for both tasks, and a minority maintains low efficiency for both.

the evolution of thresholds towards zero in chapter 3. Owing to differences in stimulus perception among individuals, threshold reinforcement led to relatively high levels of worker specialization. These results are an example of how the behavioral mechanism on which selection acts is of importance for the outcome of evolution (McNamara & Houston 2009), particularly when self-organization takes place (Bonabeau et al. 1997, Duarte et al. 2011, chapter 2).

Table 4.2: Values of mean ± SD worker specialization, mean λ ('learning') and mean φ ('forgetting') achieved at the end of evolutionary simulations, for different parameter combinations.

p_G	p_L	mean specialization, D	mean λ	mean φ
0.2	0.2	0.93 ± 0.01	0.60 ± 0.12	1.50 ± 0.05
0.2	1.0	0.94 ± 0.01	0.58 ± 0.16	1.50 ± 0.05
1	0.2	0.06 ± 0.01	3.67 ± 1.29	0.02 ± 0.00
1	1	0.86 ± 0.02	0.06 ± 0.02	1.31 ± 0.06

In the first scenario, the emergence of specialization through positive feedback ('learning') required small initial differences between individuals. These differences were present in the asynchronous updating of the stimulus levels for the individuals. With synchronous update, the presence of high values of 'learning' does not result in worker specialization. It is important to note that seemingly trivial details of the implementation (such as those allowing individual variation to arise) may have major implications for the outcome of a model.

The other scenarios consider direct selection on worker specialization. The second scenario encompasses a direct cost to switching, where individuals must wait for a few time steps before being allowed to switch tasks. This simulates a travelling cost between task locations. In the third scenario, worker efficiency in removing task stimulus increases with experience (EEP model). In both of these scenarios we found that worker specialization evolved via threshold reinforcement. In the presence of switching costs both 'learning' and 'forgetting' evolved. Threshold differentiation was produced when 'learning' was high and 'forgetting' was comparatively lower, a result that is qualitatively in agreement with Theraulaz et al. (1998).

In the model with EEP, only 'forgetting' evolved in the simulations where specialization arose. Worker specialization was favored under the parameter combinations where the probability to lose experience was larger or equal to the probability of gaining it. When the probability to lose experience was markedly smaller than the probability to gain it, then worker specialization was not adaptive, because individuals can increase efficiency on both tasks if they switch randomly. In the future it would be interesting to also consider asymmetries between tasks, e.g., different efficiency gain curves for different tasks.

The co-evolution of 'learning' and 'forgetting' only occurred under switching costs. All other situations where worker specialization evolved required only the evolution of one of the reinforcement parameters. In the first model, specialization was an indirect product of selection for minimized idleness. Under high 'learning' only, a large part of the individuals developed low thresholds for both tasks; this would have had negative fitness consequences in the model with switching costs and in the EEP model, but it had no impact on the baseline model. In the model with switching costs, since individuals were already working with maximal efficiency, colonies needed only to maximize the amount of work performed by avoiding switching and lowering their thresholds in order to become active at lower stimulus levels. Hence, it was necessary for both 'learning' and 'forgetting' to evolve under these circumstances. In the EEP model, high 'learning' becomes detrimental when specialization is beneficial, because since individuals start out with low efficiencies, there is enough stimulus present during the first time steps to make individuals switch tasks and thus develop similar thresholds for both tasks. If only 'forgetting' is low, individuals become either specialized for one of the tasks or very lazy (Figure 4.4A).

The effect of the fitness function differed slightly between the two implementations of benefits of specialization: in the implementation with switching costs, the fitness function in fact selected for the number of acts performed, because individuals had identical efficiencies throughout the simulation; in the EEP model it selected for the amount of stimulus removed. These two traits (number of acts and amount of stimulus removed) are obviously correlated, but, in the EEP model, because individuals start off with very low efficiencies, the priority for selection is to increase individual efficiencies, instead of increasing the number of acts performed by individuals – in fact, an increase in efficiency results in individuals having to perform a task less in order to remove task stimulus. If the fitness function would have selected directly for number of acts in both models, as it does in chapter 3, we would have seen different results in the EEP model. Very likely no specialization would have arisen, due to selection for increased number of acts, and hence for low efficiency. This would not make much biological sense, and would fail to address the question of how the trade-off between two tasks (in terms of efficiency gain) may lead to division of labor.

Finally, from an empirical perspective, there is some evidence that experience increases the probability that individuals will perform a task again (Weidenmüller 2004, Ravary et al. 2007), and that efficiency increases with experience (Johnson 1991, Langridge et al. 2008, Weidenmüller et al. 2009). However, to our knowledge, it has not been shown in the same species that experience leads to higher tendency to perform a task and to higher efficiency. It would also be important to investigate whether the role of experience in driving behavioral differentiation is a general phenomenon or circumscribed to the few species where it has been found. It would be interesting to compare the influence of experience in task performance in related species that differ in their degree of sociality, such as Halictine bees (Schwarz et al. 2007). We can expect the behaviour of eusocial species, due to the need of coordinating with numerous nestmates, to be more flexible and more influenced by experience than solitary or subsocial insects, which may be more canalized in their behavior.

Supplementary material

Here we provide more information regarding the simulations presented in the main text, and show results for different parameter values and implementations of the stimulus update.

A. Optimal work ratio biased towards task 1

We can examine the effect of selection for different work distributions (proportion of work performed for the two tasks) by changing the fitness function (eq. [4.2]) in the following way:

$$W=\sqrt{w_1^{\beta}w_2^{1-\beta}}, \tag{S4.1}$$

where β indicates the relative importance of the different tasks (see chapter 3 for full justification). In the main text, the fitness function corresponds to when $\beta=0.5$. If $\beta=0.75$, the optimal work distribution is biased towards task 1, which should be performed

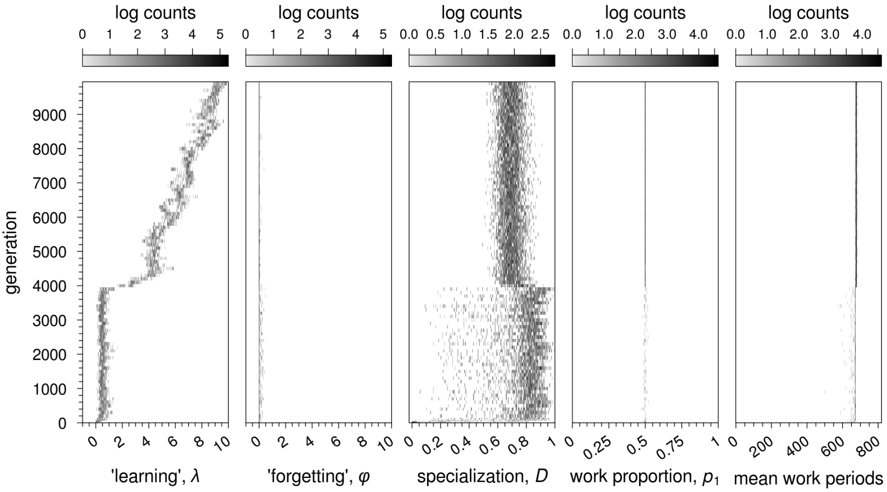

Figure S4.1: Representative evolutionary simulation of the reinforced threshold model without EEP. Graphical conventions as in main text. β=0.75 and c=0. Other parameters as in Table 4.1.

three times more than task 2. As observed for the fixed response threshold model, an asymmetric work distribution could not be obtained in the reinforced threshold model (Figure S4.1). We had not expected to obtain a 3:1 work ratio, because the key constraints observed in chapter 3 are still present in this model: the stimulus dynamics and the threshold mechanism itself, even though individual thresholds may change during a simulation. The simulations with β=0.75, in all other aspects, obtained similar results to the simulations presented in the 4 main text, where β=0.5.

B. Higher switching costs

In the main text we present results for c=0 and c=2. We also ran simulations for c= 4,6,8, and 10. Results for higher switching costs were qualitatively similar to those obtained for c=2. The main difference was that 'learning' reached higher values for higher switching costs (Figure S4.2).

C – Stimulus update implementations

The update of stimulus values, in the simulations presented in the main text, is done immediately after an individual performs a task ("individual update"). Hence, individuals first assessed for task choice, during a time step, are typically exposed to higher stimulus levels than individuals that are assessed last. To avoid an effect of assessment order across time steps, we randomize the order of individuals at the beginning of every time

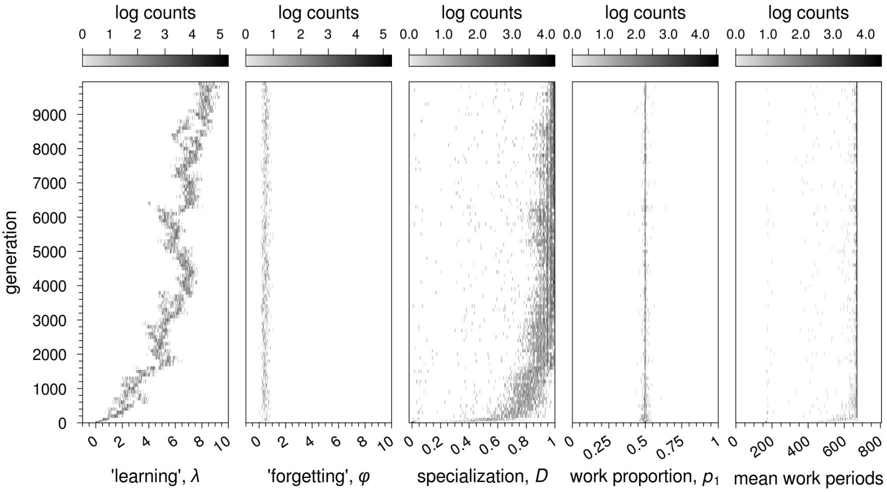

Figure S4.2: Representative evolutionary simulation of the reinforced threshold model without EEP. Graphical conventions as in main text. $\beta = 1$ and $c = 10$. Other parameters as in Table 4.1.

step. However, we found that in the reinforced threshold model without EEP, when $\lambda > 0$, differences in the stimulus encountered initially may lead to differentiation of thresholds and hence to relatively high worker specialization (Figure 4.2A in the main text). To confirm if this was indeed due to the effect of order assessment in the initial time steps, we ran simulations for a different implementation of the stimulus update. In these simulations, stimulus is updated simultaneously for all individuals ("simultaneous update"), at the end of every time step. Hence, all individuals encounter the same stimulus level (plus some noise) in a time step. The simulations ran for one generation only, each simulation having 10 colonies, with all individuals in a simulation initialized with the same values of λ and φ. We tested a range of combinations of λ and φ, and examined the level of mean worker specialization obtained. We ran simulations with the same parameter combinations for the "individual update" implementation.

Figure S4.3 shows the level of mean worker specialization found for these different parameter combinations and implementations. In the "simultaneous update" implementation we observe, as expected, no worker specialization when 'forgetting' is lower or equal to one. In the "individual update" implementation we observed that, in agreement with our evolutionary simulations, values of 'learning' larger than zero are enough to produce some worker specialization, even when 'forgetting' is zero. Similarly, worker specialization also arises when 'learning' is zero and 'forgetting' is larger than zero.

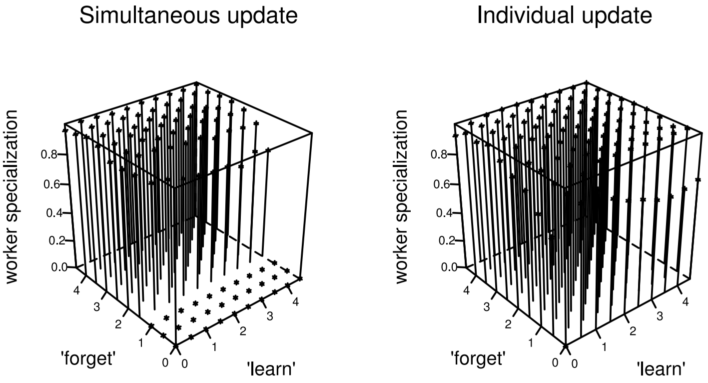

Figure S4.3: Mean worker specialization plotted against the reinforcement parameters λ, ‘learning’, and φ, ‘forgetting’, for simulations of the reinforced threshold model (without EEP, $c = 0$). Each point is an average of 10 colonies. Other parameters as in Table 4.1 in the main text.

In the model with EEP, we do not observe a qualitative difference in mean worker specialization depending on the stimulus update implementation (Figure S4.4). In agreement with our simulations, ‘forgetting’ must be larger than one in order for worker specialization to arise. ‘Learning’ does not have an effect on its own (if ‘forgetting’ is smaller than one), because individuals start off with low efficiencies and thus are unable to remove much of the stimulus. Hence, initial differences in stimulus perception are negligible in the EEP model when only ‘learning’ is large.

D – Effect of p_G and p_L on fitness

We observed that worker specialization arises and ‘forgetting’ evolves under most of the combinations of p_G and p_L tested. The exception to this was when p_L was much smaller than p_G : worker specialization does not evolve and ‘learning’ increases to high values. However, the absence of worker specialization in the latter case does not reflect a lower fitness (Figure S4.5). In fact, all colonies achieve slightly higher fitness when p_L was markedly smaller than p_G. This is because individuals can obtain maximal efficiency for both tasks (see main text) when the probability to lose efficiency is much smaller than the probability to gain it.

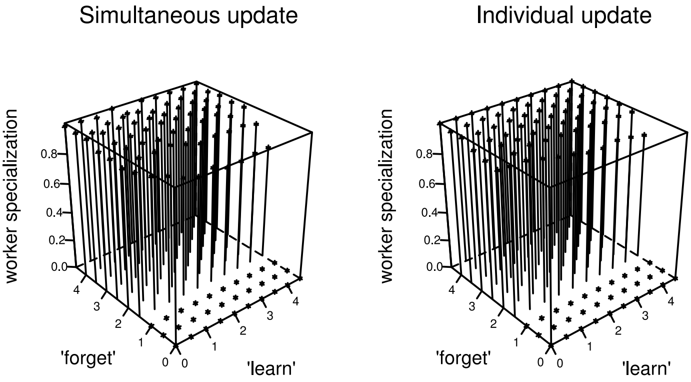

Figure S4.4: Mean worker specialization plotted against the reinforcement parameters λ, 'learning', and φ, 'forgetting', for simulations of the reinforced threshold model with EEP. Each point is an average of 10 colonies. Other parameters as in Table 4.1 in the main text.

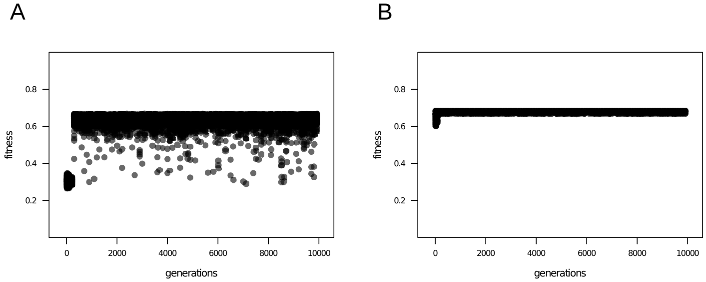

Figure S4.5: Fitness values over evolutionary time, in two representative simulations. Each point represents one colony in the population. Fitness is shown as the proportion of the maximal possible fitness which is achieved by colonies. (A) $p_G = 1, p_L = 1$. (B) $p_G = 1, p_L = 0.2$.

Box 1

How to choose between tasks: Implementation details in the response threshold model

Ana Duarte

Introduction

The idea encapsulated in the response threshold model is fairly simple and intuitive: individuals possess thresholds of response to varied task-related stimuli; if a stimulus is above an individual's threshold, the individual will be more likely to perform it. However, there are several different ways to actually implement this idea in a simulation, and different implementations may lead to different outcomes.

A potentially important implementation detail is how individuals choose between tasks when all stimuli stand above the corresponding response thresholds. The original response threshold model by Bonabeau et al. (1996) avoided a potential tie between tasks by allowing individuals to assess only one task (randomly chosen) at a time. Hence, individuals could only become motivated to perform one of the tasks. From hereon, this type of implementation will be referred to as "random task encounter". In our implementation (see chapter 3), we allow individuals to assess all task stimuli. If all stimuli are above the individual's response threshold, one task is chosen at random. From hereon, this implementation is called "tie-breaking by random choice". Yet another implementation has been used by Jeanson et al. (2007) where the individuals, after assessing all stimuli, choose the task for which the difference between stimulus and threshold is largest. This implementation shall be referred to as "tie-breaking by largest difference".

Methods

Simulations of the work phase were run for the three implementations described above. In each simulation, there were 100 colonies with 100 workers each. Colony founders were initialized from a normal distribution where each threshold had a mean 10 and standard deviation 0.5. Workers were initialized by inheriting thresholds from parents (see chapter 3 for details), with a mutation probability of 0.1 and mutation step size of 0.1. At the end of the work phase, the simulations were stopped (hence, no evolution took place).

The effect of yet another implementation detail was tested in these simulations, namely the effect of noise in stimulus perception. In half the simulations, stimulus was perceived by individuals with noise (i.e., a value drawn from a normal distribution of mean 0 and standard deviation 1 was added to the stimulus). In the other half of the simulations, no noise was added to the stimulus. All other implementation details followed chapter 3.

Results

Stimulus and worker dynamics were not affected by the implementation details (Figure Box 1.1). In all simulations, the number of workers allocated to each task was similar. The end level of mean worker specialization, however, differed between the

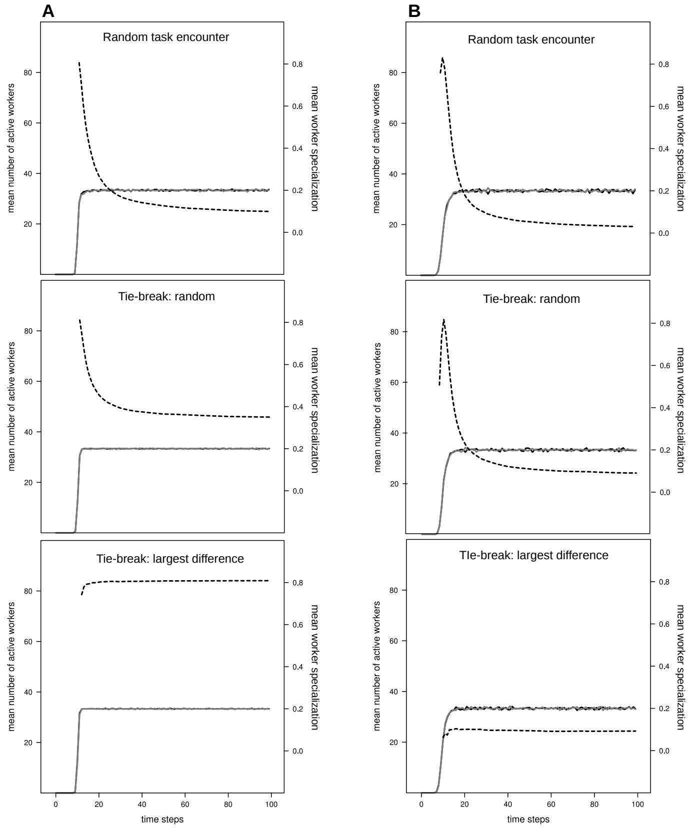

Figure Box 1.1: Response threshold model under three different implementations: random task encounter, tie-breaking by random task choice and tie-breaking by largest difference. A) Stimulus is perceived without noise. B) Stimulus is perceived with noise. Averaged for 100 colonies, the number of active workers for task 1 (black solid line) and task 2 (grey solid line) is indicated by the left-hand vertical axis, over the time steps of the work phase (horizontal axis). Worker specialization (dashed black line), also averaged over 100 colonies over the time steps, is indicated in the right-hand vertical axis.

three implementations, particularly when stimulus was perceived without noise (Figure Box 1.1A). At the end of the simulations, the mean value worker specialization was lowest in the random task encounter implementation (mean and standard deviation, 0.1±0.04), achieving higher levels under the tie-breaking by random task choice implementation (0.4±0.24). Under the tie-breaking by largest difference, mean worker specialization was quite high (0.8±0.1). Differences between these implementations, however, disappeared when noise was added to the perception of stimulus (Figure Box 1.1B). Mean and standard deviation of worker specialization, across 100 colonies, was: random task encounter – 0.03 ± 0.02; tie-breaking by random choice – 0.1 ± 0.08; tie-breaking by largest difference – 0.1 ± 0.08.

The difference between implementations, in the absence of noise in stimulus perception, can be understood in the following way. Individual differences, despite being small, are expressed perfectly in the implementation with tie-breaking by largest difference. Since both tasks are performed by the same number of workers, stimulus levels remain also at the same level for both tasks (not shown). Hence, also the differences between stimulus and threshold remain stable over time, and individuals tend to perform the same task. Obviously, if individuals had identical thresholds, specialization would break down. In the implementation of tie-breaking by random choice there is still scope to express individual differences, to some extent, but much more (non-random) variation would be required to produce high levels of worker specialization. In this implementation, the tie-breaking mechanism introduces a level of noise which breaks down specialization. As for the random task encounter, individual differences are masked by the fact that individuals cannot assess all stimuli at once. The addition of noise to the actual stimulus value also masks differences between individuals.

Discussion and conclusion

When an individual is motivated to do different tasks, the mechanism through which it decides between those tasks is of great importance. One of the mechanisms we implemented here lead to higher levels of emergent specialization, in the absence of any evolutionary advantage to specialization and under restricted genetic variation. This observation leads to the question of whether division of labor could be a secondary effect of selection for a particular tie-breaking mechanism, rather than a direct outcome of selection for worker specialization. For example, in a situation where homeostasis is important (e.g., maintenance of nest temperature), a mechanism that decides between tasks by choosing the most “urgent” one may be more efficient, thus having a fitness advantage over random choice. More work is required to establish if this is the case. However, the presence of noise destroys the effect of the different tie-breaking mechanisms on specialization, and is likely to also bring the different mechanisms closer in terms of efficiency.

Throughout this thesis we use a tie-breaking mechanism which relies on random choice, but we also assume that stimuli are perceived with noise. We conclude that, under our assumptions, our results would not have been qualitatively altered by using one of the other mechanisms for choosing among tasks. Nevertheless, in the future it would be interesting to investigate further the effect of the tie-breaking mechanisms in worker specialization.

Chapter 5

Implications of behavioral architecture for the evolution of self-organized division of labor

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Abstract

Division of labor has been studied separately from a proximate self-organization and an ultimate evolutionary perspective. We aim to bring together these two perspectives. So far this has been done by choosing a behavioral mechanism *a priori* and considering the evolution of the properties of this mechanism. Here we use artificial neural networks to allow for a more open architecture. We study whether emergent division of labor can evolve in two different network architectures; a simple feedforward network, and a more complex network that includes the possibility of self-feedback from previous experiences. We focus on two aspects of division of labor; worker specialization and the ratio of work performed for each task. Colony fitness is maximized by both reducing idleness and achieving a predefined optimal work ratio. Our results indicate that architectural constraints play an important role for the outcome of evolution. With the simplest network, only genetically determined specialization is possible. This imposes several limitations on worker specialization. Moreover, in order to minimize idleness, networks evolve a biased work ratio, even when an unbiased work ratio would be optimal. By adding self-feedback to the network we increase the network's flexibility and worker specialization evolves under a wider parameter range. Optimal work ratios are more easily achieved with the self-feedback network, but still provide a challenge when combined with worker specialization.

Introduction

Division of labor is ubiquitous in nature. The major evolutionary transitions, such as the separation of germ and soma and the transition from prokaryotes to eukaryotes, were accompanied by an increase in division of labor (Szathmáry & Maynard Smith 1995). The transition from solitary to eusocial in insects encompasses the evolution of a reproductive caste and a sterile worker caste. Furthermore, division of labor among sterile workers also evolved, in which different groups of workers specialize in different functions, such as foraging and brood care (Oster & Wilson 1978). Colony growth and survival is strongly dependent on the coordinated interaction of a large number of workers. This non-reproductive division of labor is therefore often considered a major determinant of the ecological success of eusocial insects and will be the focus of the work presented here.

Empirical evidence suggests that eusociality has evolved in associations of close kin (Boomsma 2007, Boomsma et al. 2011). Variation in behavioral tendencies can be found in forced associations of non-social individuals, leading to incipient forms of division of labor Fewell & Page 1999, Jeanson et al. 2008). Undoubtedly, a source of variation is key to generating consistent inter-individual differences and task specialization (Duarte et al. 2011, chapter 2). The questions that arise are how and why such variation arises among close kin. Here we explore some of the mechanisms and conditions through which task specialization can evolve in groups of related individuals.

Recent work on division of labor in insect societies has focused on the self- organization properties of colony behavior. According to a variety of models (Franks & Tofts 1994, Bonabeau et al. 1996, Theraulaz et al. 1998, Page & Mitchell 1998, Johnson 2009) colony properties emerge from the behavior of individual workers whose reactions to the environment is governed by simple rules. The behavioral rules leading to emergent specialization are probably shaped by natural selection (Bonabeau et al. 1997, Page & Mitchell 1998), yet only few studies have focused on the evolution of these rules (e.g., Waibel et al. 2006, Tarapore et al. 2009). Previous work focusing on the benefits of task specialization in other systems (e.g., enzyme-substrate specialization, coordination in co-viruses) generally disregard the mechanisms underlying it, viewing 3 instead specialists and generalists as fixed behavioral strategies (Wahl 2002, Tannenbaum 2007). It is thus important to develop models that integrate the evolutionary and self-organization perspective, in order to create a better understanding of division of labor and its evolution (Duarte et al. 2011).

In previous work, we took the response threshold model (Bonabeau et al. 1996) as a starting point for an evolutionary model for division of labor (Duarte et al. in press). In the response threshold model, individuals compare an environmental stimulus for a task with their response thresholds; they perform the task if the stimulus is above their threshold, otherwise they remain idle. Using this predefined behavioral architecture, we allowed the evolution of threshold values and showed that division of labor can evolve from a homogeneous population via evolutionary branching, but only if there are clear fitness benefits of individual specialization. Our work also revealed that the response threshold model has the drawback that it imposes severe constraints on the distribution of workers over tasks.

Here we look at a more flexible behavioral architecture that is represented by a simple artificial neural network (ANN). ANNs simulate the processing of stimuli by individuals, from stimulus perception by receptor nodes to effector nodes determining the behavioral output (Ghirlanda & Enquist 1998, Haykin 1999). ANNs have been used in evolutionary robotics to understand the evolution of communication and cooperation (Floreano et al. 2007, Mitri et al. 2009, 2011). In a recent paper, Lichocki et al. (2012) showed that ANN's, in comparison to response threshold mechanisms, allow for more efficient worker allocation through task switching. Here we examine the effect of the architecture of ANN's in worker specialization and worker allocation, in a context where task switching is detrimental.

In the response threshold model, the response to task-associated stimuli is determined by task-associated thresholds. The stimuli, which reflect the colony's need for work on the various tasks, change dynamically due to two factors: there is an inherent tendency for the stimuli to increase, and they are decreased whenever the corresponding task is performed. We keep most assumptions of the threshold model but allow the task-associated stimuli to be processed by an ANN. In principle both the architecture of the network and the way information is processed could evolve (Fogel et al. 1990, Yao 1999), however, we for simplicity, we focus on predefined architectures (with a fixed number of receptor and effector nodes) and allow only for the evolution of connections between the nodes. The stimuli are processed by an ANN consisting of two receptor nodes and two effector nodes (Figure 5.1). In a second part of our study, we keep the same network structure but allow for the evolution of a feedback from the effector nodes to the processing of the stimuli (Figure 5.1C). In other words, an effect of previous experience on current decisions can evolve. An effect of previous experience on task preference, leading to division of labor, has been observed in natural colonies (Ravary et al. 2007), thus it would be interesting to observe under which circumstances it could evolve.

We investigate if these slightly more sophisticated mechanisms for processing input allow for the evolution of adaptive division of labor. More precisely, we study whether task specialization among workers can evolve and moreover, whether an appropriate distribution of workers over tasks can be achieved. Throughout, the main question is whether, and to what extent, the evolution of self-organized division of labor is determined by the underlying architecture of behavior.

Model

The general aspects of the model follow Duarte et al. (in press). We consider a population of M colonies, each founded by a single-mated individual that produces N workers (typically $M=100$, $N=100$). Each colony goes through a work phase consisting of T time steps ($T=100$), where all individuals perceive stimuli associated with two tasks and decide whether to perform one of the tasks or remain idle. The amount of work performed and the distribution of workers over tasks determines the fitness of a colony, which corresponds to the number of reproductives produced. Selection occurs because the colonies of a given generation are founded by pairs of reproductives produced in the previous generation. Hence colonies where the workers perform their tasks in the most efficient and coordinated way spread the genes of their foundresses most effectively.

In line with Bonabeau et al. (1996), we assume that there are two tasks and two task-associated stimuli. Stimuli increase each time step by a fixed amount δ and decrease by an amount α whenever a worker performs the task, following ($\delta=1$ and $\alpha=0.03$ in our simulations). In the response threshold model, the association between stimuli and task was also expressed in the fact that individuals were more likely to perform a task for which the stimulus was high. However, in the present model, this is not necessarily the case. An association between task and stimulus is present because the performance of a given task decreases a given stimulus. Workers are assessed in random order and, once an individual works, the corresponding stimulus value is immediately decreased, such that the next worker to be assessed experiences a different stimulus value.

Artificial neural networks

The first network studied is a simple feedforward network (Haykin 1999) that consists of two stimulus input nodes and two behavioral output nodes, all four nodes being connected (Figure 5.1B). Each input node perceives a task-associated stimulus with a certain error ε (drawn from a normal distribution with mean 0 and standard deviation 1). The two signals are then processed and transmitted to the output neurons, via connections with weights w_{ij} that are evolvable properties of the network. Output nodes receive a weighted sum of the stimuli, generally designated activation energy. The activation energy v_i of an output node i is thus:

$$v_i=\sum_{j=1}^{2} w_{ij}(S_j+\varepsilon_j). \tag{5.1}$$

Each output neuron is characterized by a threshold θ_i, which is another evolvable property. If the activation energy of an output neuron exceeds the threshold, the neuron is activated, meaning that an individual is willing to perform the respective task. If both output neurons are activated, one task is chosen at random. Note that the response threshold model implemented in previous work is in fact a special case of the feedforward neural network, where $w_{11}=w_{22}=1$ and $w_{12}=w_{21}=0$ (Figure 5.1A). The main difference between our feedforward ANN model and the response threshold model is thus the evolution of the connection weights that determine how incoming information is processed and interpreted. The initial values of connection weights in our simulations are: $w_{11}=w_{22}=1$ and $w_{12}=w_{21}=0$. Changes in the connection weights and thresholds take place when new individuals are produced, via mutation (see below). During the lifetime of an individual, the parameters of its network are fixed. Thus we do not consider the changing of connection weights with learning, for example.

The second network architecture studied is a recurrent network (Haykin 1999). It includes all previous nodes and connections, and in addition it has two self-feedback loops (Figure 5.1C). The activation energy in a given time step will affect the activation energy in the next time step: $v_i(t+1)=\sum_{j=1}^{2} w_{ij}(S_j+\varepsilon_j)+f_i v_i(t)$. The connection weight f_i given to the previous activation energy (from here on called the self-feedback connection) is also an evolvable property that changes through mutation and natural selection during production of new individuals. During the lifetime of individuals, however, there is no change occurring in the parameters of the networks. Self-feedback connection weights were initialized at zero, which is equivalent to the feedforward network, without any influence of past experience in current decisions.

Fitness

After the work phase, the fitness of each colony is computed based on how much work the workers performed for each task. Fitness is assumed to be proportional to the weighted geometric mean of work done for both tasks:

$$W=A_1^{\beta}\cdot A_2^{1-\beta}, \tag{5.2}$$

where A_i is the total number of acts performed for task i (Duarte et al. in press, chapter 3). We take the geometric rather than the arithmetic mean in order to ensure that fitness can only be achieved if both tasks are being performed. The weighing factor β allows us to consider the (realistic) situation that not all tasks need to be performed equally often. For the fitness function (5.2), fitness is maximized if idleness is eliminated (i.e., if A_1+A_2 is maximal) and if the workers distribute over tasks according to the ratio $A_1 : A_2=\beta : (1-\beta)$. In other words, to maximize fitness the proportion p_1 of work allocated to task 1 by the colony should be equal to β:

$$p_1=\frac{A_1}{A_1+A_2}=\beta. \tag{5.3}$$

Each generation, $2M$ reproductive offspring are produced in total in the population. Colonies contribute to the population's pool of sexual individuals in proportion to their fitness. Population size is thus fixed. The reproductive individuals then form M pairs

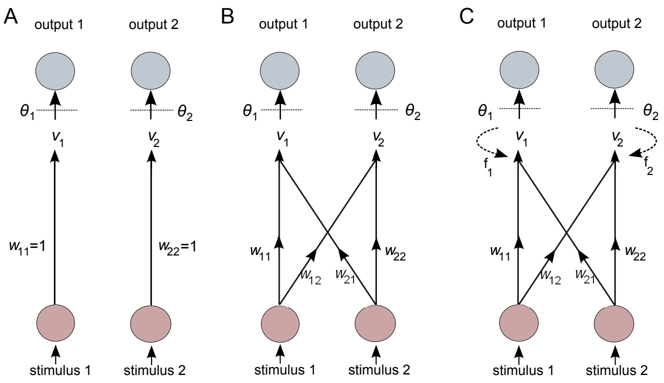

Figure 5.1: Architecture of the three types of networks. Stimulus values are perceived by input neurons. The stimuli are then processed by the network, resulting in an activation energy v for each output neuron. An output neuron is excited whenever the activation energy is larger than the neuron's threshold θ. (A) Feedforward neural network, equivalent to the architecture encapsulated in the response threshold model, where only weights w_{11} and w_{22} exist. Hence, the activation energy is equal to the perceived stimulus. (B) Feedforward neural network, fully connected. (C) Recurrent neural network, where self-feedback occurs between activation energies of previous time steps and current activation energies.

randomly. From each pair one individual will found a new colony with N workers, while the old colonies are eliminated.

Genetic details

We allowed for the evolution of all connection weights and thresholds of output nodes, giving us in a total 6 (resp. 8) evolving traits. These traits are encoded by 6 (resp. 8) gene loci. The alleles at these loci correspond to real numbers, with threshold alleles being larger or equal to zero, while connection weight alleles may also attain negative values. To keep the genetic assumptions as simple as possible, we assume that all individuals are haploid and that the network of each individual is fully determined by its genotype.

Genotypes of workers and sexuals are similarly inherited: Both types of individuals are offspring of the mated colony foundress, and possess alleles for thresholds and connection weights. Our model allows genetic linkage of the threshold loci or linkage of the connection weight loci, but both types of loci are considered to be sufficiently far apart in the genome to make them segregate independently. The degree of linkage is determined by a parameter r ($0 \leq r \leq 1$) that corresponds to a recombination rate. With probability $1-r$, the threshold alleles (resp. the connection weight alleles) are inherited as a block from one of the two parents; with probability r, the parent whose allele is transmitted is chosen independently of what happens at the other loci.

Mutation occurs with probability μ at each locus; when a mutation occurs, the genetic value at that locus is changed by adding a real number to it that is drawn from a normal distribution with mean 0 and standard deviation σ_μ. In our simulations, we typically used $\mu=0.1$ and $\sigma_\mu=0.1$.

Measuring worker specialization

We evaluate colony-level characteristics such as the proportion of work devoted to each task and the level of individual specialization. For each individual we calculate at the end of a simulation the fraction q of time steps that it stayed in the same task from that time step to the next. We average q over all workers and normalize this measure by dividing $\bar{q}$ by the probability that individuals stay in the same task merely due to chance. The latter is given by $p_1^2 + p_2^2$, where p_i is the proportion of work devoted to task i. By subtracting 1 from the value thus obtained, we obtain a measure of worker specialization that ranges between -1 and 1 (Duarte et al. in press):

$$D=\frac{\bar{q}}{p_1^2+p_2^2}-1. \tag{5.4}$$

When D is close to 1, there is a high degree of division of labor, and individuals stay in the same task much more often than expected by chance. If D is close to zero, workers switch between tasks at random. If D is lower than zero, individuals switch task more often than expected by chance.

Switching costs

Worker specialization can be adaptive if there is a cost to switching tasks (such as a time cost if tasks are confined to different locations, or a cognitive cost), or if specialized workers perform their task with higher efficiency (Smith 1776). Here we implemented a time cost scenario, by imposing c time steps of inactivity whenever an individual chooses to switch from one task to the other.

Results

Simulations of the neural network model, with different network architectures were ran for $\beta=\frac{1}{2}$, $\beta=\frac{3}{4}$ and switching costs c ranging from 0 to 5 time steps. We also tested the influence of recombination between the loci coding the neural network in the evolution of specialization. There were 10 replicates per parameter combination. The evolutionary patterns of the components of the neural networks were examined (thresholds of output neuron and connection weights) at the population level. Overall, connection weights were far more important than the thresholds in determining the behavior of networks. Hence we do not address here the evolutionary trajectories of threshold loci for the feedforward network. These can be found in the Supplementary Material A.

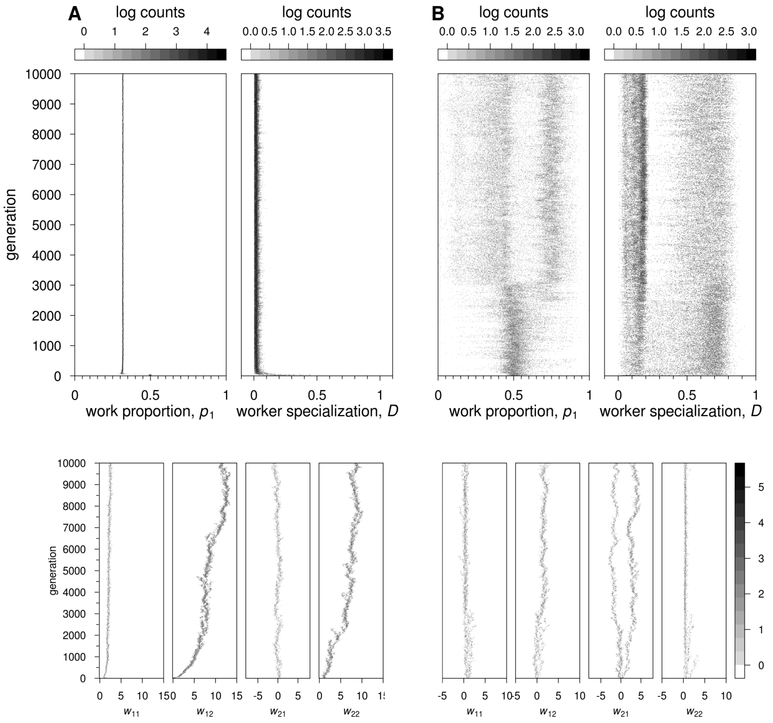

Figure 5.2: Feedforward neural networks: evolutionary dynamics of two representative simulations, for $\beta = \frac{1}{2}$ and $r = 0.5$. Grey scales indicate log counts of colonies with the corresponding value of p_1, D (scales on top of the respective graphs) and connection weights (scale on the bottom right-hand side). (A) No switching costs ($c = 0$). Top graphs: p_1 decreases to approximately 0.3. Worker specialization remains at zero. Bottom graphs: incoming connection weights at output node 2 evolve to strong positive values, whereas incoming connections weights at output node 1 evolve to weak positive values (w_{11}) or oscillate around zero (w_{21}). (B) With switching costs ($c = 2$). Top graphs: the distribution of workers over tasks and the degree of worker specialisation are both highly variable across colonies. At the end of the simulation, p_1 and D are both bimodally distributed. Bottom graphs: one of the connection weights (w_{21}) branches, one branch having positive values and the other, negative values. All other connections show weak positive values or remain very close to zero, all being relatively homogeneous in the population.

Feedforward network

Optimal worker distribution 1:1

When $\beta = \frac{1}{2}$, both tasks are equally needed, and a 1:1 distribution of workers over tasks would be optimal (see [5.3]). It is therefore somewhat surprising that, in the absence of switching costs, all replicate populations evolved a work distribution where one of the tasks was performed three times more often than the other (Figure 5.2A, top panel). From here on we refer to the task performed most often as the "preferred task". Which task was preferred varied among replicate populations, but within a population all colonies preferred the same task. Variation among colonies in fitness values was small; all colonies reached approximately 94% of the maximum fitness (see Figure S5.3). Higher fitness values could not be achieved due to the deviation from a 1:1 task distribution.

Typically in our simulations, both 'incoming' connection weights of one of the two output neurons (the neuron corresponding to the preferred task) became positive over evolutionary time (Figure 5.2A, bottom panel). As for the incoming connections of the other output neuron (corresponding to the non-preferred task), the direct connection (w_{11} in the example simulation of Figure 5.2A) became positive, while the cross- connection (w_{21}, in Figure 5.2A) typically became weak, oscillating between positive and negative values. In all simulations, the strongest positive connection was between the stimulus input neuron of the non-preferred task to the output neuron of the preferred task (w_{12}, in Figure 5.2A). Hence, individuals use the stimulus for one task (their non-preferred task) to motivate them for performing the other task (their preferred one). As a consequence, they continue performing their preferred task, even if the stimulus level of this task has become very low (Figure S5.2). For this parameter combination ($\beta = \frac{1}{2}$, $c = 0$), the degree of recombination had no effect on the outcome of the simulations (Figure S5.4A).

In the presence of switching costs, the results are considerably different. When switching costs were low ($c = 1$), worker specialization only evolved in the absence of recombination ($r = 0$), with $61.4 \pm 7.2\%$ of the colonies (mean±SD) evolving values of $D > 0.5$. When $c = 2$, worker specialization also evolved in the presence of recombination (Figure 5.2B). Here $35.6 \pm 8.2\%$ of the colonies showed $D > 0.5$. In all simulations with $c \geq 2$ there was a clear (but weak) positive relationship between colony fitness and the degree of worker specialization within the colony; colonies with high mean specialization have a fitness advantage of approximately 20% over non-specialized colonies (Figure S5.3).

The bias in favor of one of the tasks that was observed in the absence of switching costs was much less pronounced or even absent in the presence of such costs. For $c = 2$, initially most colonies show a work distribution close to 1:1 (Figure 5.2B, top panel). After about 3500 generations, a new pattern arises, with part of the colonies having a pronounced bias toward task 1, while the other colonies have a bias toward task 2. The simulation shown is representative for higher switching costs ($c \geq 2$), but to a certain extent the outcome depends on the detailed assumptions. If, for example, recombination was not allowed in the simulation of Figure 5.2B (i.e., $r = 0$), three different types of colonies evolved (with $p_1 = 0.4$, $p_1 = 0.5$, $p_1 = 0.6$, respectively; see Supplementary Material A and Figure S5.4B).

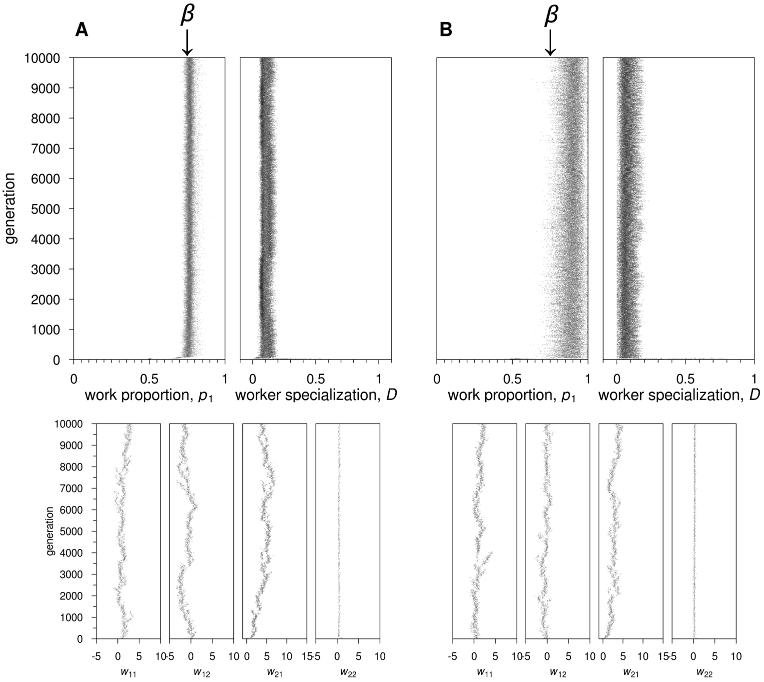

Figure 5.4: Feedforward neural networks: evolutionary dynamics for two representative simulations, where $\beta = \frac{3}{4}$ and $r = 0.5$. The same graphic conventions as in Figure 5.2 are followed. (A) $c = 0$. Top graphs: p_1 increases to the optimal value 0.75; specialization remains low. Bottom graphs: connection weights incoming at output node 1 become positive (strongest connection weight being w_{21}); connection weights incoming at output node 2 become negative (w_{12}) or positive, but very close to zero (w_{22}). (B) $c = 2$. Top graphs: p_1 increases to values above 0.75; D remains low. Bottom graphs: similar to when $c = 0$, but w_{22} is closer to zero.

The neuronal connection weights linking input neurons to the corresponding output neurons (i.e., w_{11} and w_{22}) tended to evolve positive values, between 0 and 4 (Figure 5.2B, bottom panel). One of the cross-connections (i.e., w_{12} or w_{21}) showed evolutionary branching (Geritz et al. 1998), that is, polymorphism evolved from an initially monomorphic state. Figure 5.2B is representative in that w_{21} branches into a bimodal

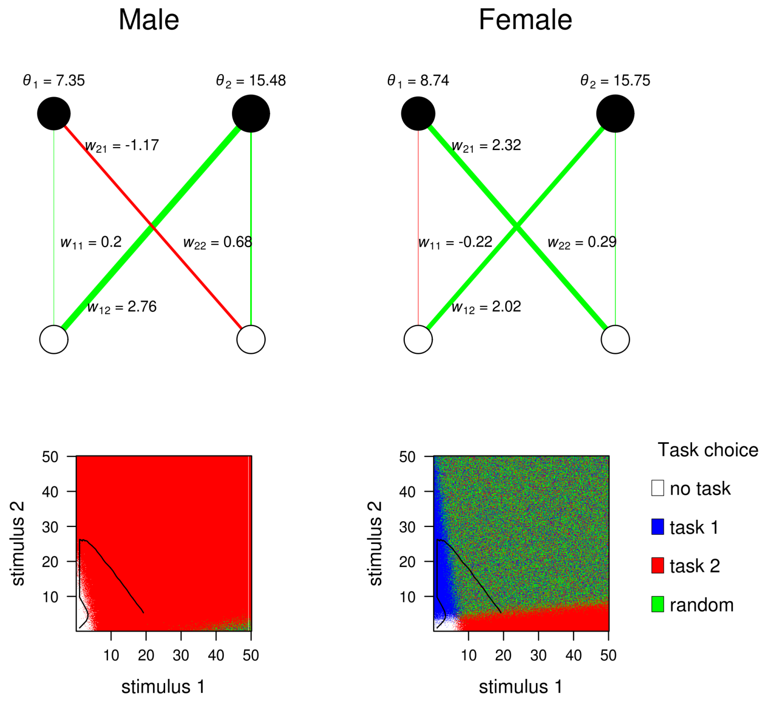

Figure 5.3: Evolved feedforward neural networks of a highly specialized colony. In specialized colonies, the networks of the two parents (arbitrarily labelled 'male' and 'female') differ from each other in a systematic way. Top panels: for each parent, the evolved values of the connection weights and thresholds of the network are shown. Bottom panels: the stimulus-response characteristics of each network type are shown. For each combination of stimuli, the bottom graphs show whether the network is motivated to perform only task 1 (blue), only task 2 (red), both tasks (green; in this case, one task is chosen at random), or none (white). The trajectory of stimulus values from the start to the end of the work phase, in the last generation of the evolutionary simulation, is indicated in black. Starting values were $S_1 = S_2 = 0$. Other parameter values as in Figure 5.2B.

distribution, with one branch becoming negative and the other positive. When such branching occurs, two distinctly different types of networks coexist in the population (Figure 5.3, top panel). This is crucial for worker specialization: a high degree of specialization only occurred in colonies where the two parents differed in the sign of one of their cross-connection weights. From Figure 5.3 we can deduce how specialization occurs in a colony with dissimilar parents. The key difference between the parents' networks is the genotypic value of w_{21}, which determines that one parent (arbitrarily labelled 'male') is a specialist for task 2, while the 'female' shows a large area of the stimulus space where both tasks are activated and where accordingly one of the two tasks is chosen at random (Figure 5.3, bottom panel). The workers produced by these parents will be divided among those two phenotypes. Stimulus increase initially occurs for both tasks, until the stimuli levels reach a region where individuals with a positive w_{21} will perform task 1. As a consequence, only stimulus 2 will keep increasing, until an area is reached where individuals with a negative w_{21} will start performing task 2. The decreasing stimulus of task 2 means that fewer workers will do task 1, because the main motivating force to do task 1 is the positive w_{21}. Hence, stimulus for task 1 will also increase. Individuals are then in an area of the stimulus space where half of them will work randomly on either task, while the other half will only perform task 2.

For $0<c\leq 3$, branching occurred at only one of the cross-connections, while for $c>3$ both cross-connections branched in some of the simulations. In the absence of recombination, evolution leads to a higher degree of worker specialization (Figure S5.4B). Evolutionary branching occurs now for all the connection weights and for the thresholds as well. The area in stimulus space where networks choose both tasks is much smaller in the absence of recombination (Figure S5.5), leading to more pronounced differences between workers and, hence, more specialization. Branching of more loci means that networks will be more differentiated than seen previously for cases with recombination.

Optimal worker distribution 3:1

In view of eq. (5.3), when $\beta=\frac{3}{4}$, the optimal worker distribution over tasks is 3:1, with 4 task 1 being performed 3 times more often than task 2 (i.e., $p_1=0.75$). Populations indeed evolved a worker distribution approaching this value (Figure 5.4A, top panel). In absence of switching costs, task 1 was performed $76.7\pm0.42\%$ of the time (mean±SD across all replicate populations, for $r=0.5$). All colonies attained more than 99% of maximum fitness, with a few colonies achieving the maximum (Figure S5.3).

A general pattern in the evolution of connection weights was the strengthening of the cross-connection w_{21} and the disappearance of connection w_{22} (as in Figure 5.4A, bottom panel). This explains the observed increase in performance of task 1. The cross-connections once more play an important role; since the strongest incentive to do task 1 comes from the stimulus of task 2, this allows workers to keep doing task 1 even if the stimulus for that particular task is depleted.

Worker specialization did evolve, but only in the absence of recombination ($r=0$). Even then, specialization levels of $D \geq 0.5$ were only obtained for a larger number of colonies when switching costs were high ($c \geq 3$). When worker specialization did not evolve (as in Figure 5.4B, top panel), colonies evolved work distributions even more biased than $p_1 = 0.75$. When the work distribution is that strongly biased, the probability to stick to the previous task ($p_1^2 + p_2^2$) is high even if tasks are taken on at random. Hence, by evolving a work distribution with more than 80% of the work devoted to task 1 the number of switches decreases, thus allowing colonies to avoid switching costs even in the absence of worker specialization. In this case, connection w_{22} reached lower values than for the simulations without switching costs (Figure 5.4B, bottom panel).

We tested the behavior of a more complex network, where the activation energy of an output neuron could have a feedback on the activation energy at the next time step (Figure 5.1C). The self-feedback connections were allowed to co-evolve with the rest of the network. We ran ten replicate simulations for all the parameter combinations tested above.

Recurrent network

Optimal worker distribution 1:1

In contrast to the results of the feedforward network, the optimal worker distribution $p_1 = 0.5$ was now realized in a high proportion of colonies (e.g., Figures 5.5A,B). However, this proportion decreased with increasing switching costs. For $c=0$, the proportion of colonies with $p_1 = 0.5$ was $99.9 \pm 0.3\%$ when $r=0.5$ and 100% when $r=0$. For $c=2$, this proportion was at $76.5 \pm 4.1\%$ when $r=0.5$ and $46.7 \pm 7.6\%$ when $r=0$ (mean$\pm$SD number of colonies across replicates).

When $c=0$, all colonies in all replicate simulations achieved the maximum possible fitness, indicating that all workers are active all the time (Figure S5.6). Workers switched randomly between tasks ($D=0$ for all colonies, Figure 5.5A). This was achieved by evolving positive self-feedback connections allowing workers to continue working even in the absence of an external stimulus for a task. Connection weights from stimuli input neurons to output neurons were also positive (Figure S5.7).

Worker specialization evolved already for low switching costs ($c=1$), but the behavior shown by colonies, for all $c>0$, differs considerably in the simulations in the presence or absence of recombination. In the presence of recombination, all colonies within a population reached a high value of D (Figure 5.5B). In the absence of recombination, populations typically consisted of colonies with low D and colonies with high D (Figure 5.5D). For $c=1$, for example, $25 \pm 7\%$ of the colonies (mean$\pm$SD across replicates) had $D<0.2$, while $66 \pm 7\%$ of colonies showed $D>0.5$.

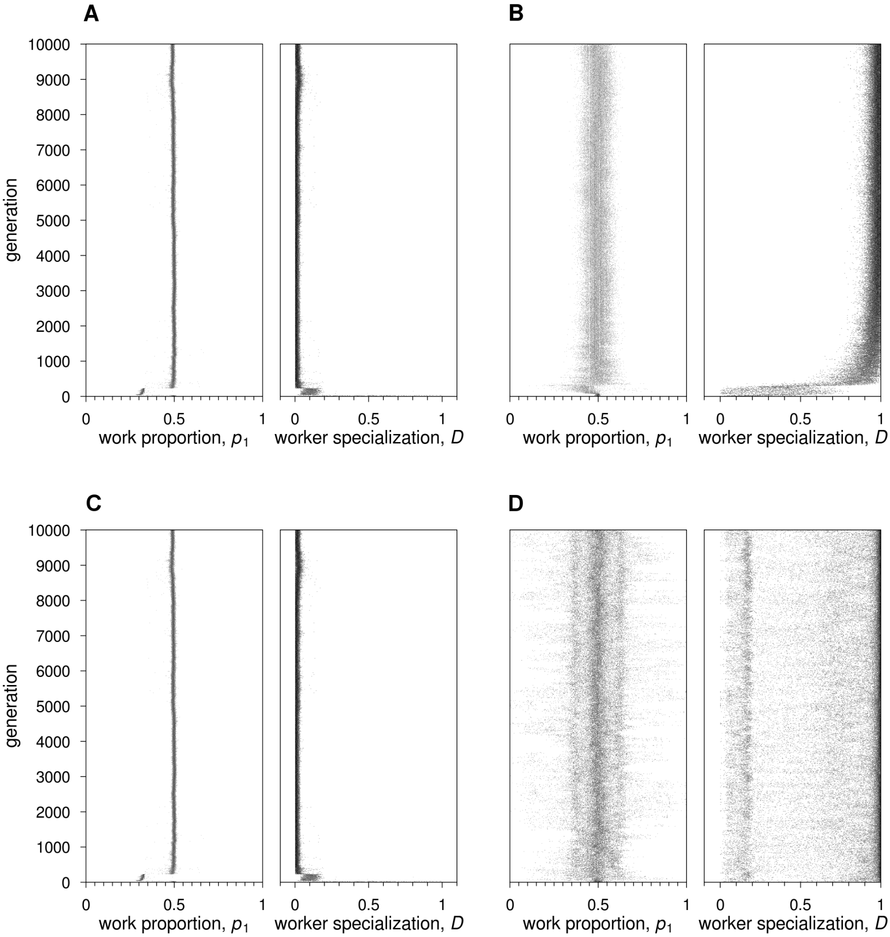

Figure 5.5: Recurrent neural networks: evolutionary dynamics of the proportion of time spent on task 1, $p1$, and the degree of worker specialisation, D. Two representative simulations are shown for $\beta = \frac{1}{2}$. (A,B) $r = 0.5$. In (A), switching costs are absent: p_1 quickly reaches the optimal value 0.5; worker specialization does not evolve. In (B), $c = 1$: p_1 becomes more variable, but still approximates the optimal value 0.5; D rapidly increases to its maximal value 1, for all colonies in the population. (CD) $r = 0$. In (C), switching costs are absent: the evolutionary dynamics is as in (A). In (D), $c = 2$: not all colonies can evolve worker specialization, and p_1 is also more variable across colonies.

In the simulations where all colonies exhibited a high level of worker specialization, self-feedback connections evolved very high positive values (as in Figure 5.6, top panel). The connection weights from task stimulus to corresponding output neuron (w_{11} and w_{22}) evolved to positive values, while cross-connection weights (w_{12} and w_{21}) evolved to negative values (as in Figure 5.6, bottom panel). In these simulations, the evolved strategy leading to division of labor uses the strong self-feedback connections, accompanied by negative cross-connection weights, to create differentiation between individuals. Since individuals from the beginning perceive different levels of stimuli, differences in activation energy will occur and will be amplified in subsequent time steps, creating consistent differences among individuals. Hence division of labor is achieved by experience-based specialization.

In the simulations where colonies differ in their degree of worker specialization, neuronal connections (including self-feedback connections) show evolutionary branching, with one branch showing positive values and the other branch negative values or values close to zero (Figure 5.7). In this case, evolutionary branching allows for the co-existence of different genetically determined specialists, as seen previously for the simpler feedforward architecture.

Optimal worker distribution 3:1

In the absence of switching costs, the mean p_1 calculated across replicates was 0.75 and, hence, corresponding to the optimal value for fitness (Figure 5.8A). Interestingly, worker specialization was negative ($D<0$) in all colonies in 19 out of 20 simulations (encompassing both simulations where recombination is present as well as where it is absent). In other words, individuals switched more often between tasks than expected by chance.

Worker specialization never evolved for $c=1$. For $2 \leq c \leq 3$, specialization only evolved in the absence of recombination. These results are shown in the Supplementary Material (section B, Figures S5.9-S5.10). For $c=3$, in two of the replicates, all colonies show high levels of specialization, accompanied by the optimal worker distribution (Figure S5.9A). In these particular replicates the self-feedback connections became strongly positive (Figure S5.11). In all other replicates only about half the colonies showed $D>0.5$, while the other half had no specialization (Figure S5.9B). The distribution of workers over tasks was highly variable, with very few colonies actually achieving $p_1=0.75$. The networks in these populations showed evolutionary branching of self-feedback connections (Figure S5.10).

For higher switching costs ($c \geq 4$), worker specialization could evolve in the presence of recombination, but only in three replicates out of 20, in the evolutionary time considered (results not shown). In these replicates, all colonies combined high levels of specialization and a work distribution very close to the optimal value of 0.75. Worker specialization was again achieved through two different types of networks; one where evolutionary branching occurs in key neuronal connections (particularly self- feedback connections), and the other through evolution of strong positive self-feedback connections (not shown). The first network type leads to a population where only half the colonies have specialized workers, and the correct work proportion is hardly achieved; the second network type leads to a population where all colonies have a high level of specialization and the optimal work proportion.

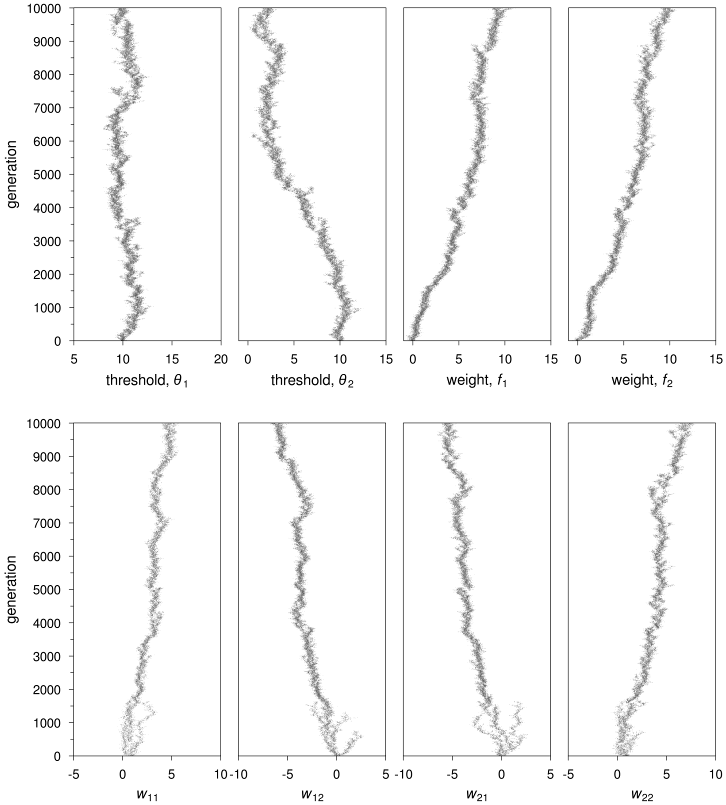

Figure 5.6: Recurrent neural networks: Evolutionary trajectories of network parameters leading to experience-based specialization. A simulation is shown in which all colonies in the population evolve high degree of division of labor. Parameter values are: $\beta = \frac{1}{2}$, $c = 3$, $r = 0$. The self-feedback connection weights, f_1 and f_2 (third and fourth graph on the top panel), increase over generations, a pattern which is found across simulations showing the same worker specialization patterns. Also representative is the pattern encountered in the other connection weights (bottom panel) is the evolution of negative values in cross-connection weights (w_{12} and w_{21}) and positive values in the connection weights between the task stimulus and respective output node (w_{11} and w_{22}).

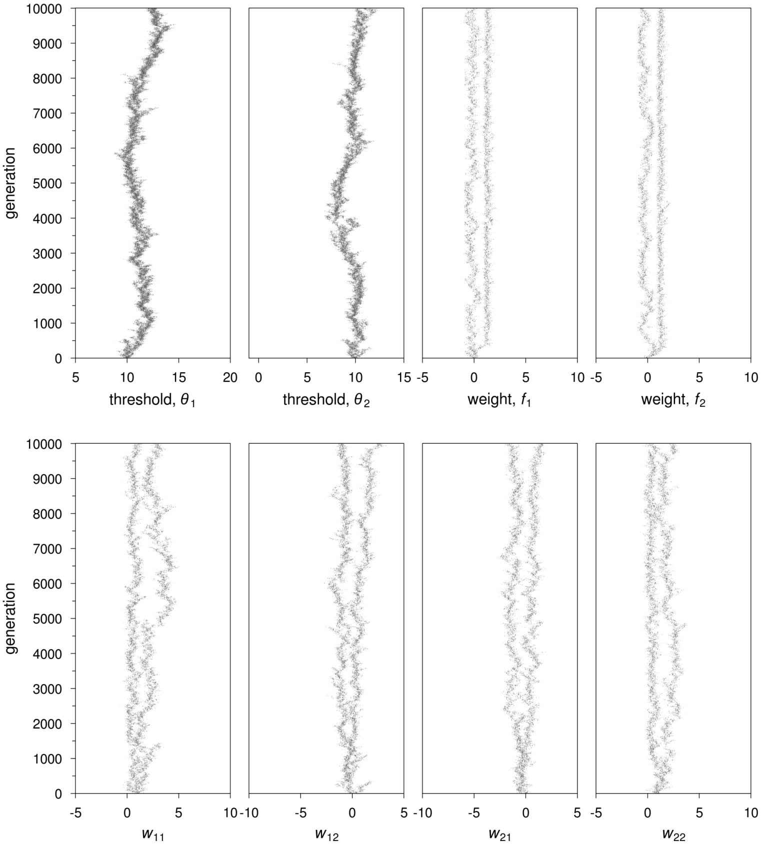

Figure 5.7: Recurrent neural networks: evolutionary trajectories of network parameters leading to genetically-determined specialization. A simulation is shown in which only half of the colonies in the population evolve a high degree of specialization. Parameter values as in Figure 5.6. All connection weights undergo evolutionary branching. The self-feedback (f_1 and f_2) and crossed connection weights (w_{12} and w_{21}) show one branch with negative values and the other with positive values. The other connection weights show one branch close to zero and the other larger, positive values.

Discussion

Here we studied whether and how two different neural network architectures enable the evolution of self-organized division of labor and adaptive task ratios. Our results are summarized in Table 5.1.

With a feedforward network (Table 5.1), worker specialization evolved more easily (i.e., at lower switching costs) in the absence of recombination. In the absence of recombination the connection weights can co-evolve as a tightly linked block of genes, making it easier to evolve specific combinations of connection weights favoring specialization. Recombination pushes populations into a solution where only one connection weight locus branches, the rest of the network being relatively homogeneous in the population. This allows worker specialization to occur, but to a lesser extent than in the absence of recombination, because at least one of the parent networks in a specialized colony behaves as a generalist for a large range of stimulus combinations. A large percentage of colonies showed no worker specialization, hence, no division of labor. This is because random mating allows for couples with similar genotypes to produce colonies where workers are too similar and therefore division of labor cannot emerge.

Previous work on the response threshold model (Chapter 3) showed that the work ratio could not easily deviate from 1:1, even if a biased work ratio was optimal. In contrast, in the case of the feedforward network, the work ratio was always biased for one of the tasks, even when a symmetric work ratio was optimal (Table 5.1). Owing to selection for minimizing idleness, the evolved networks maximized the amount of work done by using the stimulus from one of the tasks to stimulate workers to perform the other task. In this way, one of the tasks was performed in excess (the 'preferred' task), even when its associated stimulus had been depleted. Although this may seem counter-intuitive, it represents an advantage over networks that attempt to maximize both tasks, because these networks would be limited to the work strictly necessary to reduce stimuli to zero. When $\beta = \frac{3}{4}$, the optimal work ratio was achieved, but only in the absence of switching costs. When switching costs were present, the most common evolved strategy was to increase the proportion of work for task 1 in order to minimize switching among tasks.

Some of the limitations of the simple feedforward network were eliminated in the slightly more complex architecture of the recurrent network, where previous activation energies feed back on current activation energies. Worker specialization evolved at low switching costs, now both in the presence and absence of recombination (Table 5.1), at least for $\beta = \frac{1}{2}$. Interestingly, the presence of recombination favored an outcome where all colonies showed a high degree of specialization. In these populations, specialization does not depend on the presence of two complementary networks in the parents of a colony (as in Figure 5.3), but on a strengthening of the self-feedback connections. This allows for initial differences between individuals in stimulus perception to be amplified in subsequent time steps and leads to behavioral differentiation through reinforcement of previous experiences. In the presence of recombination, this strategy prevails. However, when no recombination occurs, evolutionary branching of connection weights is still the prevalent strategy through which worker specialization evolves. Why is the experience-based strategy not observed in all simulations? A likely reason is that to reach this strategy, the values of neural connections must first pass through values where, in the absence of recombination, evolutionary branching is

Table 5.1: Overview of results obtained for three different behavioral architectures: RT – response threshold model (chapter 3); FFN – feedforward neural network; RNN – recurrent neural network. Parameter combinations are indicated in the first column and first two rows. The second column indicates the result we look for: $\beta{=}p_1$ corresponds to the achievement of the optimal work ratio; $D{\geq}0.5$ corresponds to the evolution of worker specialization. In the central columns, for different levels of switching costs, c, we indicate if such results were obtained. Y indicates it was satisfied in all replicate simulations; N indicates that the result was not obtained, in the majority of simulations; P indicates that, in the majority of simulations, a fraction of the colonies within the population obtained the result.

		$r{=}0$			$r{=}0$			
Work ratio	Result	$c{=}0$	$c{=}1$	$c{\geq}2$	$c{=}0$	$c{=}1$	$c{\geq}2$	Model
$\beta{=}\frac{1}{2}$	$p_1{=}\beta$	Y	Y	Y	Y	Y	Y	RT
		N	P	P	N	N	P	FFN
		Y	P	P	Y	Y	P	RN
	$D{>}0.5$	N	P	P	N	N	P	RT
		N	P	P	N	N	P	FFN
		N	P	P^a	N	Y	Y	RN
$\beta{=}\frac{3}{4}$	$p_1{=}\beta$	N	N	N	N	N	N	RT
		Y	P	N	Y	P	N^b	FFN
		Y	P	P^c	Y	P	N^c	RN
	$D{>}0.5$	N	N	P	N	N	P	RT
		N	N	P^a	N	N	N	FFN
		N^d	N	P^c	N^d	N	N^c	RN

[a] for $c{\geq}3$
[b] except for a small percentage (<3) when $c{=}2$
[c] with exception of few simulations, where all colonies obtain the result
[d] $D{<}0$

more advantageous. Hence, the evolutionary outcome is dependent on initial conditions. We confirmed this by running simulations where the self-feedback connections were initialized at higher values (e.g., $f_1{=}f_2{=}2$); in this case all populations evolved the experience-based strategy rather than evolutionary branching (results not shown). The evolution of an experience-based strategy is affected by stochastic effects at the moment that the population passes the "branching point", namely on the direction and magnitude of genetic variation, that may lead to local fitness optima. The two strategies may thus represent alternative stable states. The mean population fitness of the genetic specialization (evolutionary branching) is noticeably lower than the mean population fitness of the experience-based strategy (Figure S5.7).

The recurrent network also allowed for the optimal work ratio to be reached in most cases, at least by part of the population (Table 5.1), even in the presence of switching costs. When $\beta=\frac{1}{2}$, the self-feedback connections allow the continuous activation of both tasks, stimulating individuals that had previously done a task to do it again, even in the absence of the corresponding task stimulus. With this architecture it is also harder to attain the optimal work ratio when $\beta=\frac{3}{4}$ and switching costs are considered, and only few replicate populations show both $p_1=0.75$ and a high degree of worker specialization.

The recurrent network has similarities with the reinforced threshold model, in which individual thresholds are lowered after the performance of the respective tasks and increased when the tasks are not performed (Theraulaz et al. 1998, Gautrais et al. 2002). In both models, initial differences in experience lead to consistent behavioral differentiation, thus bypassing the need of specific genetic combinations for the emergence of task specialization. However, in terms of the distribution of workers over tasks, the reinforced threshold model suffers from the same limitations as the fixed threshold model, with worker distribution being mainly dependent on the parameters of stimulus dynamics (Chapter 4).

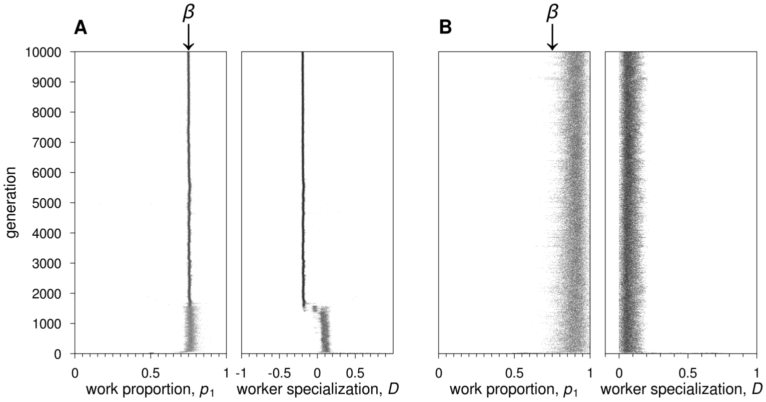

Figure 5.8: Recurrent neural networks: evolutionary dynamics of work distribution p_1 and worker specialisation D for $\beta=\frac{3}{4}$ and $r=0.5$. (A) $c=0$. p_1 quickly reaches the optimal value 0.75. D evolves to negative values, indicating that individuals switch tasks more often than by chance. (B) $c=2$. p_1 increases to values above 0.75; worker specialization does not evolve.

Our results highlight the importance of considering asymmetries in models of division of labor. In the evolutionary response threshold model in Chapter 3, we show that a biased p_1-value cannot be obtained through the evolution of thresholds. To achieve a biased p_1-value in this model, asymmetry must be present in the environment (e.g., in the values of task-associated stimuli (Bonabeau et al. 1996) to which the response-threshold mechanism then responds. However, in reality, asymmetries in the work distribution might also arise from the ability of individuals to perceive and prioritize tasks differently. Here we show that, for both types of networks studied, it is not easy to evolve strict worker specialization together with an asymmetric distribution of workers over tasks. A major difficulty is that in case of genetically determined specialization the work proportion is dependent, to a large extent, on the proportions of different specialists in each colony. Since we only consider single-mated foundresses, colonies in our model show either equal proportions of the two specialist strategies or only one of the specialist strategies. Evolving experience-based specialization enables an asymmetric work distribution and division of labor (although at a lower degree of worker specialization than under symmetric conditions, and only in the absence of recombination), yet the trajectory towards this strategy is subject to stochastic effects that may diverge evolution towards genetically determined specialization or towards an increase of performance of the most needed task beyond its optimal level.

The observed difficulty in favoring a specific work ratio under switching costs indicates that the simple behavioral architectures investigated are limited in the ability to evolve efficient solutions to complex optimization problems. In the presence of switching costs, it is important for colonies to maximize worker specialization, while at the same time minimizing the number of idle workers *and* optimizing the work ratio. The behavioral architectures considered thus far were only able to evolve sub-optimal solutions to this multi-faceted problem.

Modelling the evolution of behavioral mechanisms by means of artificial neural networks presents several advantages when compared to *a priori* chosen behavioral architectures such as a response threshold mechanism. First, mechanisms potentially leading to self-organized division of labor are not built into the model, but must emerge from the model. Second, evolving neural networks transcend some limitation of the human mind. When asked to design plausible mechanisms, the imagination of most modellers is limited to simple and intuitive mechanisms (like a response-threshold mechanism) that our mind can easily envisage. For example, it is unlikely that one would envisage a mechanism where a task-associated stimulus does not stimulate the performance of its corresponding task, but of a different one, as it occurs in the feedforward network. By using an independent modelling setup, we can get an idea whether, and to what extent, the results based on the more standard implementations are robust. In our case, the simple feedforward network is too constrained to achieve worker specialization and an appropriate distribution of workers over tasks. By adding a simple elemental feedback the resulting recurrent network had a much higher evolutionary potential. In future models we could consider the evolution of the network's topology, e.g., by allowing the addition and elimination of neurons and connections to an existing network through mutation (Yao 1999).

The simple feed-forward neural network was constrained by a problem already present with the response threshold mechanism: to get specialization at the colony level, the coexistence of two specialist genotypes is necessary. Random mating and recombination played an important role in the evolutionary outcome. In general we observed that recombination made it more difficult for genetic specialization to evolve. With recombination, evolutionary branching at multiple loci occurred only rarely, at very high switching costs. This is in accordance with the argument that, in constant environments, recombination may destroy favorable allelic combinations (Feldman et al. 1996, Otto & Michalakis 1998). Our model suggests that in systems where strong genetic task determination and high recombination rates exist, multiple mating would be favored, in order to increase the chance that workers have favorable allelic combinations. This is in accordance to what we observe in honeybees (Palmer & Oldroyd 2000, Wilfert et al. 2007). Under the recurrent network architecture, recombination may also play a beneficial role by creating more genetic variation in the self-feedback connections, which could favor division of labor emerging through the experience-based strategy.

The purpose of our approach was not to represent the behavioral architecture of real organisms, but to present a conceptual model that could shed some light on the role of architectural constraints in the evolution of self-organized division of labor. A limitation of this approach is that the larger the network, the more difficult it is to draw conclusions that are biologically relevant. We have implemented two very simple networks, and yet already have six to eight evolvable parameters. We were able to understand the interaction of the networks with the environment and pinpoint the key connections that allowed for specific behaviors, but this may not be possible for more complex architectures.

The fitness function used (eq. [5.2]) favored the minimization of idleness. Although it is not unrealistic to assume that more work will translate to higher colony productivity, in reality social insect colonies contain a large proportion of idle workers (Schmid-Hempel 1990, Thomas & Elgar 2003, Dornhaus et al. 2008). Examples of circumstances that would allow the presence of idle workers include environmental perturbations that require quick recruitment of "stand-by" workers, advantage of energy-saving strategies under poor resource conditions, and selective neutrality of "incompetent" workers due to highly redundant organization of work (Schmid-Hempel 1990) (and references therein). As stressed before, here we present a conceptual model for the effect of behavioral architectures in division of labor, and necessarily simplify certain assumptions. A more realistic version of our model would treat fitness as the number of offspring produced by a colony, and explicitly consider the nature of the different tasks (e.g., foraging and brood care).

Division of labor is a broad topic, with many aspects that were outside the scope of this study. Previous theoretical work has focused on the evolution of differentiated multicellularity, the evolution of germ and soma in multicellular organisms, and the effect of developmental plasticity in gene expression as a cause of individual differentiation (Pfeiffer & Bonhoeffer 2003, Schlichting 2003, Michod 2007, Gavrilets 2010). Here we focused on the evolution of behavioral task specialization in groups where reproductive altruism (analogous to germ-soma differentiation) has already evolved, an assumption which is in line with a recent comparative analysis of the evolutionary history of division of labor (Simpson 2012). We did not consider the role of developmental plasticity, although this plays an important role in the differentiation of morphological castes (Oster & Wilson 1978). Underlying the different questions concerning division of labor, however, is a problem of functional optimization: Organisms can increase their reproductive success if they perform different tasks efficiently. Dividing tasks among lower-level units within the organism or colony (often referred to as a superorganism) is a solution to the problem. What our model suggests is that the particular behavioral rules through which task specialization arises may impact the evolutionary outcome.

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Supplementary Material

A. Feedforward neural network

Worker specialization and work distribution when $\beta = \frac{1}{2}$ As shown in the main text (Figure 5.2), the feedforward neural networks have several limitations. One of them is that work proportion tends to be biased towards one of the tasks, instead of matching the optimal value ($p_1 = \beta$).

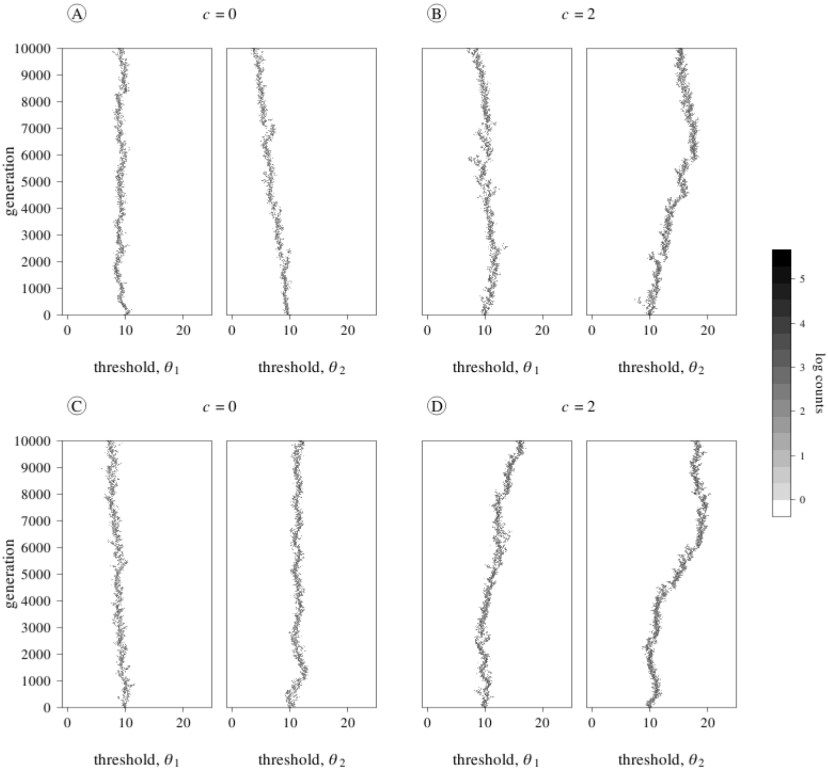

Figure S5.1: Evolutionary trajectories of thresholds for four example simulations differing in the switching costs and the optimal work proportion, β. Graphic conventions follow Figure 5.2 in the main text. In all simulations, $r = 0.5$. (A) $\beta = \frac{1}{2}$, $c = 0$. (B) $\beta = \frac{1}{2}$, $c = 2$. (C) $\beta = \frac{3}{4}$, $c = 0$. (D) $\beta = \frac{3}{4}$, $c = 2$.

In Figure S5.1 we show the evolutionary trajectories of the thresholds in the neural network in a representative simulation (also represented in Figure 5.2A). In agreement with what can be observed in Figure 5.2A of the main text, where the proportion of work is biased towards task 2, the threshold for task 2, θ_2, decreases over evolutionary time in the absence of switching costs (Figure S5.1A). The threshold for task 1, θ_1 seems to be changing only due to drift. This may further facilitate the performance of task 2, but the main determinants of the network's behavior were the connection weights, particularly the cross-connection weights.

In Figure S5.2, we show the stimulus and worker dynamics in a typical colony during the work phase, in the last generation of an evolutionary simulation (corresponding to Figures 5.2A and S5.1A). The number of workers engaged in task 2 are, on average, 66.7 ± 4.1 (mean±sd over the last 90 time steps). On average 33.3 ± 4 workers perform task 1. Stimulus levels for both tasks reflect this: while stimulus 1 reaches higher levels (due to fewer workers removing this stimulus), stimulus 2 is maintained at 1. This val-

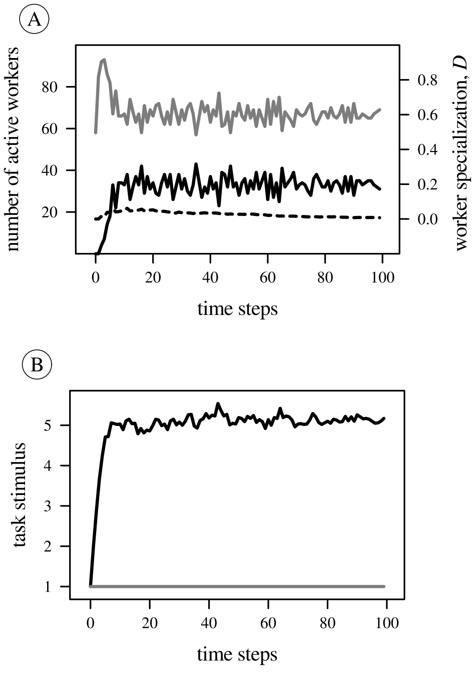

Figure S5.2: Typical colony in the last generation of an evolutionary simulation ($c = 0$ and $\beta = \frac{1}{2}$). (A) Number of workers engaged in task 1 (black solid line) and task 2 (grey line) are indicated on the left-hand vertical axis, during time steps of the work phase. Degree of worker specialization, D (black dashed line), is indicated on the right-hand vertical axis. From the start, more workers engage in task 2 than task 1. Worker specialization close to zero throughout the simulation. (B) Stimulus for task 1 (black line) and task 2 (grey line) during the time steps of the work phase. Stimulus 1 remains at higher values, due to the fewer number of workers performing task 1.

ue is exactly the value of stimulus increase which is added every time step (we account stimulus values after all changes in stimulus take place). Hence, the stimulus which is added every time step is completely removed. From previous work in the response threshold model, from where we adopted our assumptions on within-colony dynamics, we know that the added stimulus, δ, is removed when δ/α workers are engaged in the

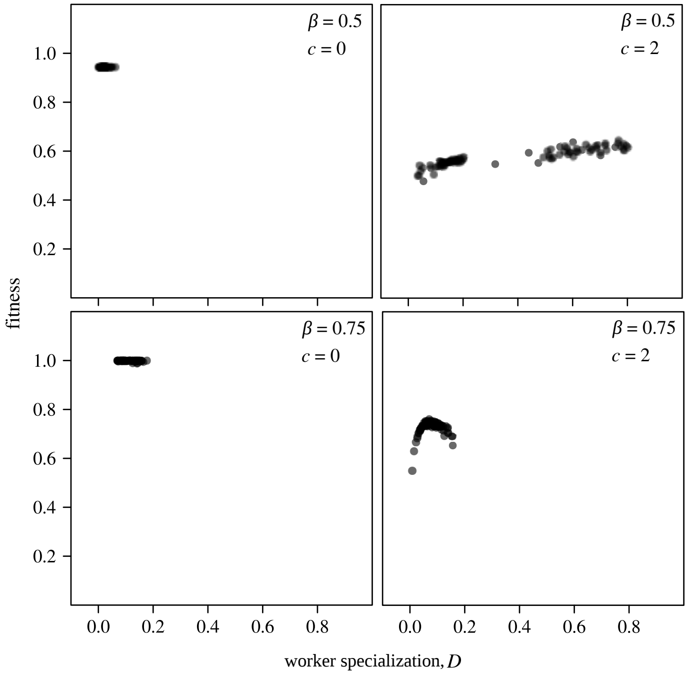

Figure S5.3: Relationship between colony fitness and worker specialization at the end of evolutionary simulations of the feedforward network in the absence (A,C) and presence (B,D) of switching costs. For all colonies, fitness is represented as the fraction of the maximum possible fitness. In (A,B), $\beta = \frac{1}{2}$. (A) $c = 0$, corresponding to Figure 5.2A in the main text. All colonies achieve a high fitness; despite the fact that the evolved distribution of workers over tasks deviates substantially from the optimum value $p_1 = 0.5$ (see Figure 5.2 in the main text). As expected in absence of switching costs, there is no relationship between colony fitness and D. (B) $c = 2$, corresponding to Figure 5.2B in the main text. Colony fitness increases with worker specialization, but even for large values of D colony fitness is substantially lower than in the absence of switching costs. In (C,D), $\beta = \frac{3}{4}$. (C) $c = 0$, corresponding to Figure 5.4A in main text. All colonies achieve the highest possible fitness, because they are now able to achieve the optimal ratio among tasks (3:1). As expected in absence of switching costs, there is no relation between fitness and D. (D) $c = 2$, corresponding to Figure 5.4B in main text. Colonies do not reach high D, yet fitness changes with D in a non- monotonic way.

task (see Chapter 3). Since worker task choice happens sequentially and stimulus is immediately affected by the work performed, many workers in our simulation inevitably choose task 2 when $S_2 = 0$. This is made possible by the fact that a positive weight connected stimulus 1 to output node 2 (as in Figure 5.2A), hence motivating individuals to keep working for task 2 when stimulus 1 is high.

The limitations of the feedforward neural network prevent the colonies from achieving the maximum possible fitness. Figure S5.3 illustrates the magnitude of this deviation. Maximum fitness is achieved when workers are never idle and distribute over tasks according to $A_1 = \beta N$ and $A_2 = (1-\beta)N$. If A_1 and A_2 are the actually observed averages of the numbers of workers performing each of the two tasks per time step, relative colony fitness (i.e., colony fitness divided by maximum fitness) is given by:

$$\frac{W}{W_{\max}} = \left(\frac{A_1}{\beta N}\right)^{\beta} \left(\frac{A_2}{(1-\beta)\,N}\right)^{1-\beta}. \tag{S5.1}$$

This value is plotted in Figure S5.3 as a function of worker specialization, D. In order to minimize initialization effects, the averages A_1 and A_2 were calculated on basis of the last 90% of the work phase. Figure S5.3 shows that in the absence of switching costs (top left-hand graph) colonies are penalized for not reaching the optimal work distribution $p_1 = 0.5$ (see Figure 5.2 in the main text and Figure S5.2).

In the presence of switching costs, colonies are also unable to reach the optimal work proportion of 0.5 (Figure 5.2B in main text). Hence, colonies are penalized in fitness (Figure S5.3, top right-hand graph) for not having the optimal work proportion and for the enforced periods of idleness associated with switching between tasks. There is nevertheless a clear, yet weak, relationship between worker specialization and fitness, indicating that worker specialization allows colonies to recover some of the fitness lost due to switching costs.

Worker specialization and work distribution when $\beta = \frac{3}{4}$ When the optimal work proportion is biased towards one task and $c = 0$, colonies are able to reach maximal fitness (Figure S5.3, bottom left graph), because they can evolve the optimal work proportion and eliminate idleness. When switching costs are present, worker specialization could not evolve (with recombination). However, individuals could still avoid some of the switching costs by performing mostly task 1. Fitness levels are thus not as low as one could expect (Figure S5.3, bottom right graph).

Role of recombination Changing recombination rate had an important effect in the outcome of the model. In this subsection we consider only $\beta = \frac{1}{2}$. In the absence of recombination, worker specialization evolved more easily, from $c \geq 1$. Higher levels of worker specialization were also obtained than in the presence of recombination (Figure

S5.4B, top panel). All the connection weights of the neural networks showed evolutionary branching (Figure S5.4B, bottom panel), whereas in the presence of recombination this only occurred for one of the connection weights.

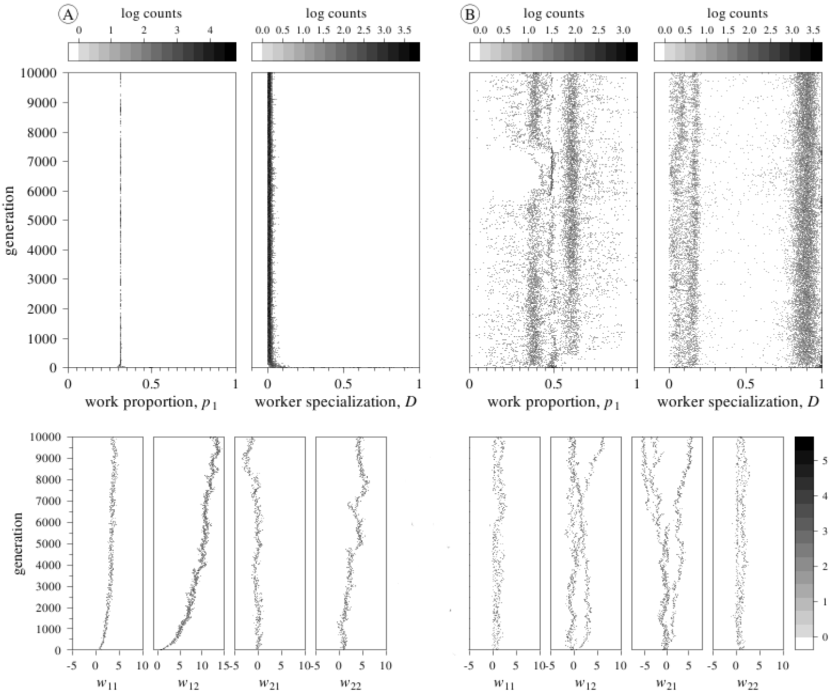

Figure S5.4: Evolutionary dynamics of two representative simulations of the evolution of a feedforward neural network, for $\beta=\frac{1}{2}$ and $r=0$. The figure follows graphic conventions of Figure 5.2 in the main text. (A) $c=0$. Top graphs: p_1 evolves to approximately 0.3. Worker specialization remains at zero. Bottom graphs: connection weights linked to output neuron 2 increase to positive values, the strongest being the cross-connection w_{12}. Direct connection weight w_{11} becomes positive, while the cross-connection w_{21} evolves to negative values. (B) $c=2$. Top graphs: p_1 becomes more variable, with some colonies achieving the optimal value, 0.5, but most falling in one of two regions, one close to 0.4, the other close to 0.6. D rapidly evolves to a bimodal distribution with approximately 70% of the colonies having $D>0.75$ and approximately 30 % having $D<0.2$. Bottom graphs: all connection weights suffer evolutionary branching. The cross-connections diverge the most, with one branch showing positive values and the other negative values.

Since all connection weights showed evolutionary branching, evolved networks can differ more strikingly than in the presence of recombination. In Figure S5.5, we show the parent networks of a highly specialized colony, at the last generation of an evolutionary simulation, under switching costs. The behavior of the networks is remarkably complementary, with the male network specializing in task 2 and the female network in task 1.

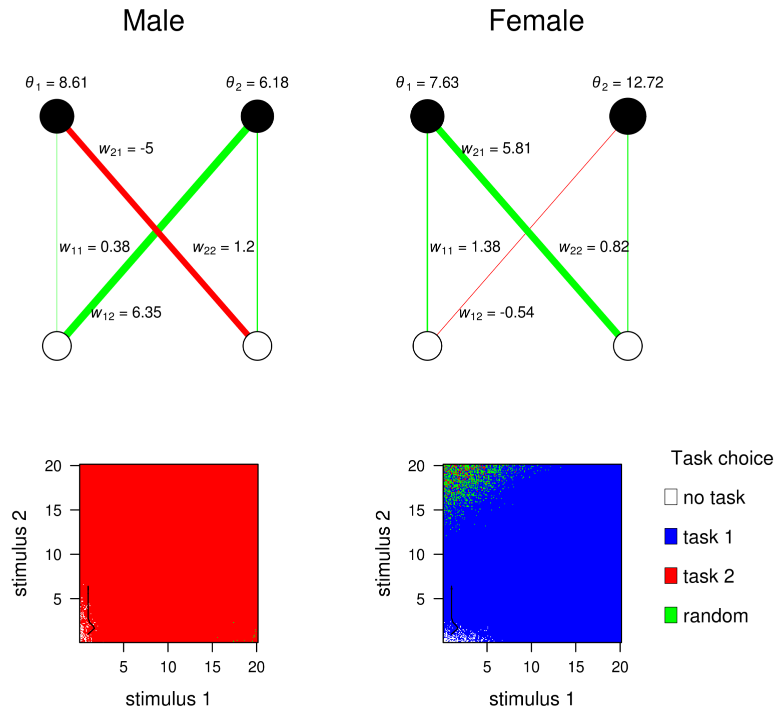

Figure S5.5: Evolved feedforward neural networks of the parents of a highly specialized colony in the simulation corresponding to Figure S5.4B (last generation). Top panels: evolved values of connection weights and thresholds are shown for each parent. Bottom graphs: the stimulus-response characteristics of each network are shown. For each combination of stimuli, the bottom graphs show whether the network is motivated to perform only task 1 (blue), only task 2 (red), both tasks (green; in this case, a task is chosen at random) or none (white). The black line indicates the trajectory of stimuli values during the work phase of the last generation of the evolutionary simulation. Starting values were $S_1 = S_2 = 0$.

B. Recurrent neural networks, with self-feedback

Worker specialization and work distribution when $\beta = \frac{1}{2}$ When the possibility for a self-feedback is included in the network architecture, many of the limitations of the previous architecture are eliminated. In the absence of switching costs, colonies always evolve positive connection weights and self-feedback (Figure S5.7). In the presence of recombination, it is now possible for all colonies to reach the highest possible fitness, both when switching costs are absent and present (Figure S5.6, top graphs). The variation found in fitness under switching costs (Figure S5.6, top right) can be explained by a larger number of colonies deviating from the optimal work proportion (Figure 5.5B in main text).

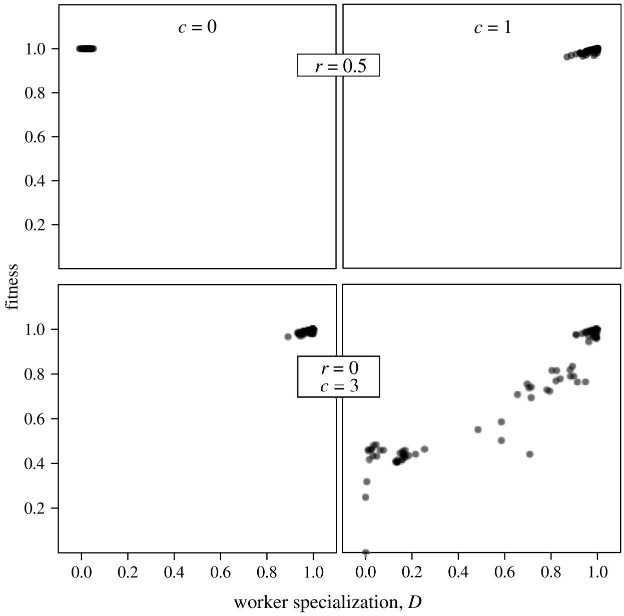

Figure S5.6: Relationship between relative fitness and worker specialization, D, at the last generation of four representative simulations of the evolution of recurrent neural networks, for $\beta = \frac{1}{2}$. (A) $c = 0$, $r = 0.5$: corresponding to Figure 5.5A in the main text. All colonies reach the highest possible fitness. (B) $c = 1$, $r = 0.5$: corresponding to Figure 5.5B in the main text. All colonies have high degree of worker specialization ($D > 0.8$). Colonies with the highest level of worker specialization are able to reach also the highest possible fitness. (C) $c = 3$, $r = 0$: corresponding to Figure 5.6 in main text, one of the few cases in the absence of recombination where all colonies evolve worker specialization, and achieve maximum fitness. (D) Same parameter combination as (C), but depicting the more general pattern found in the absence of recombination and presence of switching costs (corresponding to Figure 5.7 in the main text). Only a portion of the colonies reach high worker specialization, which results in high variation in fitness among colonies.

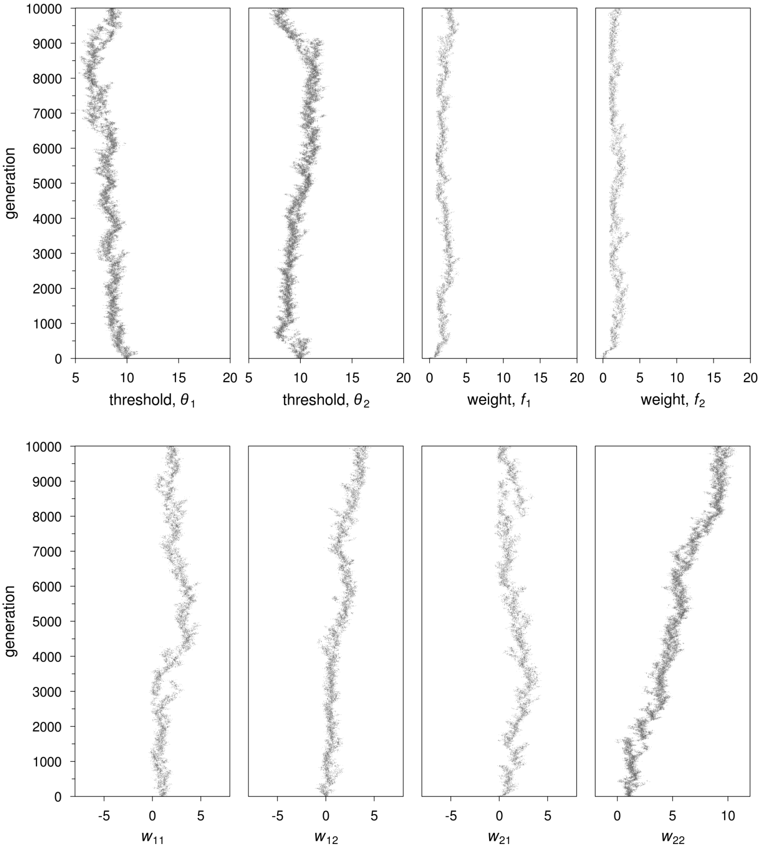

Figure S5.7: Evolutionary trajectories of thresholds and connection weights of recurrent networks, in a simulation with $c=0$, $r=0.5$ and $\beta=\frac{1}{2}$, corresponding to Figure 5.5A in main text.

Worker specialization and work distribution when $\beta=\frac{3}{4}$ When $\beta=\frac{3}{4}$ and $c=0$, colonies can also evolve easily the optimal work proportion, as shown in the main text. In the presence of switching costs, the outcome depended on whether there was recombination or not. In the presence of recombination, evolution of worker specialization rarely occurred. In the absence of recombination, worker specialization was again achieved via two different strategies. In a few simulations, all colonies showed $D \geq 0.5$, and obtained values of p_1 near the optimal, as in the example of Figure S5.8A. In the majority of simulations, populations showed two types of behaviour (Figure S5.8B): work more often for task 1, showing no worker specialization; or work for the two tasks in the same proportion, and divide labour, with high worker specialization. The first strategy, where all colonies show relatively high *D*, is obtained by increasing the self-feedback connection weights (Figure S5.11), whereas the second strategy results from evolutionary branching of self-feedback connection weights (Figure S5.10). Contrasting with what occurs for $\beta = 0.5$ in the absence of recombination, the other connection weights do not typically branch in these simulations.

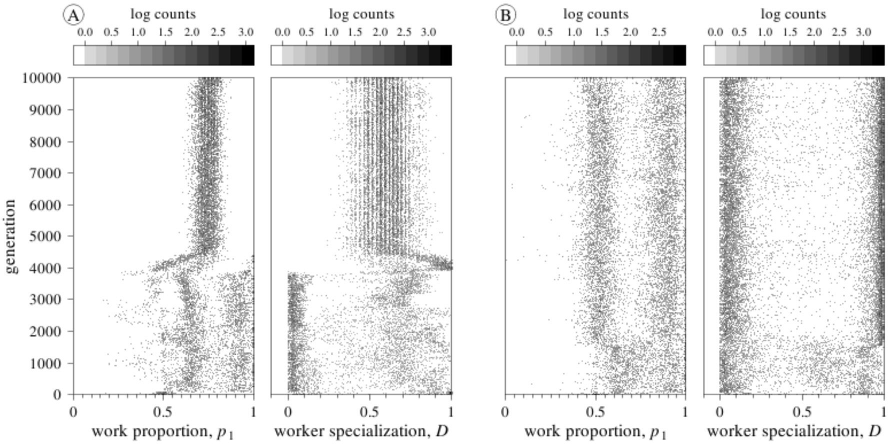

Figure S5.8: Evolutionary dynamics of two simulations of the evolution of a recurrent neural network, with self-feedback, for $\beta = \frac{3}{4}$, $r = 0$ and $c = 3$. The simulations are examples of the two strategies that evolved in response to switching costs. (A) The less frequent outcome (2 out of 10 simulations), where all colonies show values of p_1 close to 0.75, the optimal value, and most colonies show $D \geq 0.5$, at the end of the considered evolutionary time. (B) The more frequent outcome, where approximately half the colonies showed p_1 around 0.5 and $D > 0.8$, and the other half showed $p_1 > 0.75$ and $D < 0.2$.

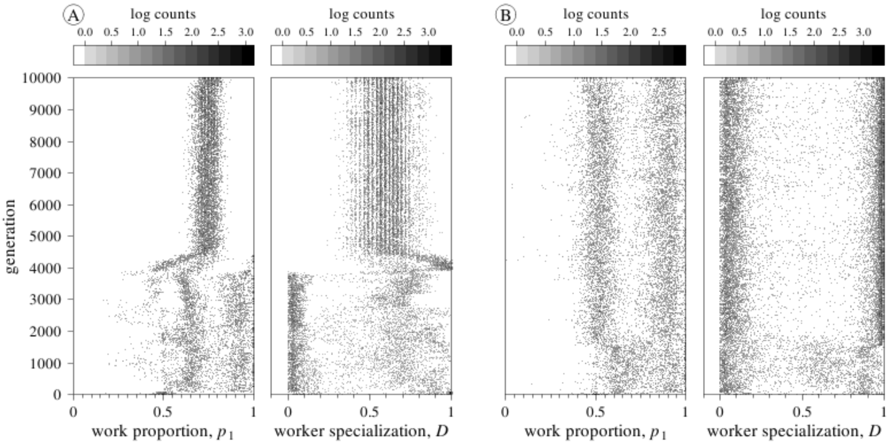

Figure S5.9: Evolutionary dynamics of two simulations of the evolution of a recurrent neural network, with self-feedback, for $\beta = \frac{3}{4}$, $r = 0$ and $c = 3$. The simulations are examples of the two strategies that evolved in response to switching costs. (A) The less frequent outcome (2 out of 10 simulations), where all colonies show values of p_1 close to 0.75, the optimal value, and most colonies show $D \geq 0.5$, at the end of the considered evolutionary time. (B) The more frequent outcome, where approximately half the colonies showed p_1 around 0.5 and $D > 0.8$, and the other half showed $p_1 > 0.75$ and $D < 0.2$.

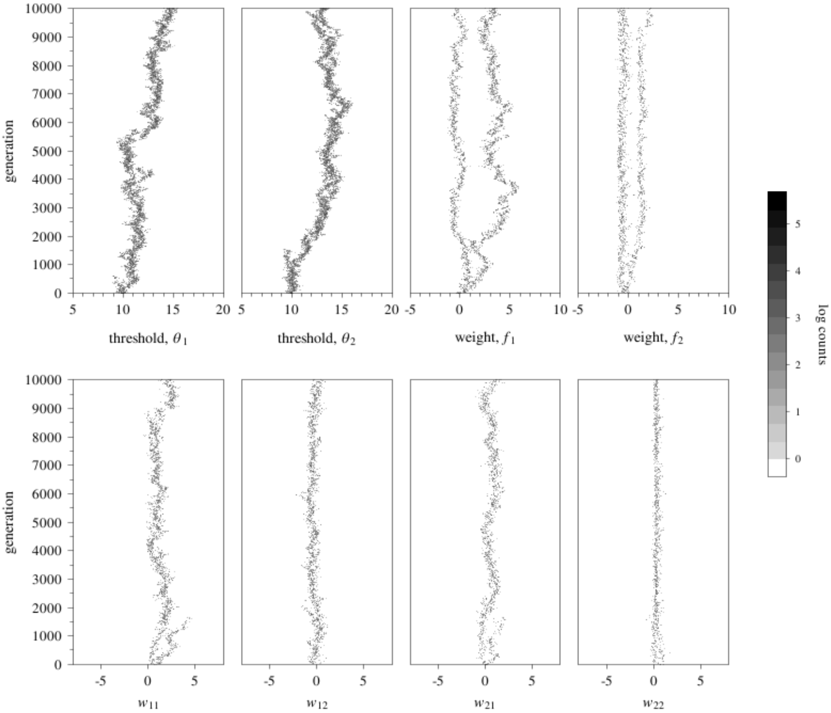

Figure S5.10: Evolutionary trajectories of thresholds and connection weights of recurrent networks, in a simulation with $c=3$, $r=0$ and $\beta=\frac{3}{4}$, corresponding to Figure S5.7B. Top graphs: self-feedback connection weights go through evolutionary branching, as in other simulations where only a portion of the colonies shows high degree of worker specialization. One branch has positive values, and the other negative values. Bottom graphs: weights are maintained at quite low values, oscillating around zero.

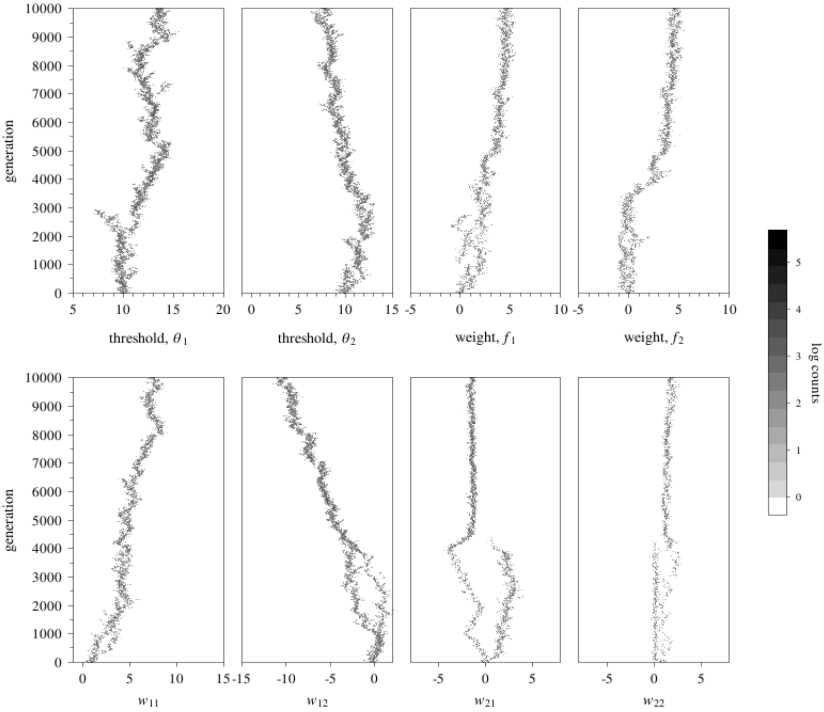

Figure S5.11: Evolutionary trajectories of thresholds and connection weights of recurrent networks, in a simulation with $c=3$, $r=0$ and $\beta=\frac{3}{4}$, corresponding to Figure S5.7A. Top graphs: self-feedback connection weights evolve positive values, as in other simulations where all colonies showed high degree of worker specialization. Evolution of thresholds did not show a specific pattern across simulations, hence it plays a less important role in the outcome. Weights showed positive values for direct connections (with $w_{11} > w_{22}$) and negative values for cross-connections (with $w12 < w21$), a pattern also representative for other simulations where all colonies evolved worker specialization.

Chapter 6

Antennal detection of task-related stimuli in workers of *Camponotus fellah*

Ana Duarte, Laurent Keller, Patrizia d'Ettorre

Unpublished manuscript

Abstract

Division of labor in social insects is crucial to their ecological success, yet the mechanism through which individuals tend to choose different tasks is poorly understood. Here we use a simple neurophysiological technique, electroantennography, to assess whether different task choice can be associated with the ability of worker antennae to detect task-related stimuli. We collected nurses and foragers from a colony of *Camponotus fellah* and tested the antennal response to different chemical stimuli: larval cuticular hydrocarbon (CHC) extracts, nestmate and non-nestmate CHC extracts and 1-octanol. We found no significant difference between foragers and nurses in the response to any of the task-related stimuli, suggesting that task choice differences stem from processes occurring in the central nervous system. However, nurse antennae reacted slightly more to air flow than forager antennae. With our experimental conditions, worker antennae did not detect larval CHC's. Both nestmate and non-nestmate CHC's were detected, with non-nestmate CHC's eliciting a higher response. We discuss the implication of these results for the ongoing debate on recognition systems in ants.

Introduction

Division of labor is considered to be determinant of the ecological success of social insects (Oster & Wilson 1978, Hölldobler & Wilson 1990, Robinson 1992). Individuals in social insect colonies tend to differ consistently in their task choice (i.e., they are, to some extent, specialized), which allows for the parallel performance of different tasks. Since colonies are typically large it is thought that individual workers do not have global knowledge of the colony's needs for the different tasks, but rather rely on local cues of task need. Division of labor must therefore arise through self-organization, emerging from the interaction among nestmates and with the local environment, with individuals obeying very simple behavioral rules (Gordon 1996, Bonabeau et al. 1997).

It has been proposed that individuals in the same colony have different thresholds of response to task-associated stimuli, an idea formalized in a few self-organization models (Bonabeau et al. 1996, 1998, Page & Mitchell 1998). According to these models, individuals with low threshold for a given task would tend to engage in that task at lower stimulus levels, thus decreasing the likelihood that individuals with higher thresholds would perform the task. Hence, individuals with low thresholds would become specialists for that task. Evidence for a threshold-like mechanism is mainly drawn from the honeybee, bumblebees and some ant species (Detrain & Pasteels 1991, Page et al. 1998, Pankiw & Page 2000, O'Donnell & Foster 2001, Weidenmüller et al. 2009). It has been shown in these organisms that genotype and development may play a role in shaping thresholds. However, the neurophysiological basis of thresholds itself is still mostly unclear.

In this study, we investigate whether differences in task choice could be related to inherent differences in the ability of the workers' antennae to detect odors associated with these tasks. In insects, olfactory receptor neurons are located in the antennae. The axons of olfactory receptor neurons go to the antennal lobes, where stimuli are primarily processed (reviewed in:Galizia & Rössler 2009, Kleineidam & Rössler 2009). Hence, the sensitivity of receptor neurons to detect certain odors may be a first step to different behaviors. For example, workers that specialize in tasks outside the nest may be more sensitive to foraging- or defense-related odors. In this study we test the ability of antennae from different workers ("nurses" and "foragers") of the ant *Camponotus fellah* to detect task-associated odors. For this purpose we use electroantennography (EAG), a technique which measures the output of the olfactory receptor neurons in response to a given odor. The odors tested were related to nursing, foraging and nest defense.

Methods

Collection of workers

Workers were taken from a laboratory colony of *Camponotus fellah*, which had been started from a mated queen collected in Israel, Tel-Aviv in June 2007. Workers observed carrying brood in the nest were considered as nurses; workers eating or close to the food source in the foraging arena were considered as foragers. In order to avoid disturbing the nest too often, while also minimizing the waiting time of workers before the EAG was performed, ants were collected in groups of two to five ants, in maximally three collection moments per day. Collection and EAG measurements took place over three days, such that in total 16 nurses and 16 foragers were measured. Workers from the same "caste" (nurse or forager) were kept together in a box lined with fluon. Each day, an equal number of foragers and nurses were analyzed, and their order randomized.

Odors

We tested the antennal response of collected workers to different substances. We used cuticular hydrocarbon (CHC) extract from larvae, as a stimulus associated with brood care. CHC extract from nestmates and non-nestmates was used as a stimulus associated with nest defense. A 0.1% solution of 1-octanol (Sigma-Aldrich) was chosen as a stimulus associated with foraging, since the colony had been previously trained to associate this smell with food (N. Bos, pers. comm.) As controls, a mechanical stimulus was used (air), and the solvents for CHC extracts and 1-octanol solution, respectively, pentane (HPLC grade, Sigma-Aldrich) and mineral oil.

Cuticular hydrocarbon extractions

For the larval CHC extracts, 20 larvae were used. Larvae were collected from the *C. fellah* colony from where workers were collected and killed by freezing at -20°C. The 20 larvae were then placed in a small glass vial and covered with approximately 400 μl of pentane, shaking the vial slightly to release CHC's, and let rest for 5 minutes. The extract was then taken up with a pipette and placed in another vial. In a pilot experiment, dichloromethane was also used for CHC extraction from larvae, but no difference was observed between the two solvents. Therefore pentane was chosen for this experiment, owing to its lower toxicity. The same method was used for extraction of CHC's of adult workers, but only 10 workers were used for 400 μl of pentane. Nestmate CHC's were extracted from workers collected from the focal colony's foraging arena. Non-nestmate CHC's were extracted from workers from a different laboratory *C. fellah* colony, also from its foraging arena. Extracts were kept in the refrigerator (4°C) when not in use in the electroantennography tests.

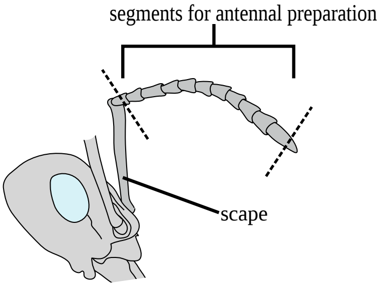

Figure 6.1: Scheme of an ant worker's head, indicating the section used for EAG preparations.

Electroantennography

The left antenna of each worker was excised with a sharp steel blade under a magnifying glass. The scape of the antenna and the first segment of the tip of the antenna were cut off (Figure 6.1), and the antenna was mounted between two glass capillaries filled with Ringer solution. The capillaries were mounted on silver electrodes. Antennal response was expressed as the total depolarization of the olfactory neurons in mV. Activity was amplified and recorded using the "EAG" software from Syntech (Hilversum, The Netherlands). 10 µl of the test solutions were applied on pieces of filter paper introduced into Pasteur pipettes, heated to approximately 50 °C. The odor was applied by blowing a pulse of carbon-filtered humidified air (250 ml min^{-1}), generated by a mechanical stimulus air controller (Syntech) through the Pasteur pipette into a tube carrying a continuous stream of carbon-filtered humidified air over the antennal preparation. A recovery period of 30 s was allowed between each stimulus. The first stimulus presented to the antennae was air (heated pipette with filter paper without any solution), and then the other stimuli (larval CHC, nestmate CHC, non- nestmate CHC, octanol, and, as control, the solvents pentane and mineral oil), in a randomized order for each antenna.

Statistical analysis

For statistical analysis the amplitude of the response to the different stimuli was measured in mm, from the graphs originated by the EAG program, for each antenna. We used the difference between the response to the chemical stimuli and the response to the mechanical stimulus (air) as the response variable in the statistical analysis, following Lopez-Riquelme et al. (2006). The data was divided and analyzed in three separate parts: response to larval CHC and its control pentane, response to adult worker CHC and control pentane, and response to 1- octanol solution and control mineral oil. This was done to prevent comparisons between stimuli with possibly different concentrations of evaporated molecules. Worker type (nurse or forager) and stimulus type were the independent variables. Model selection following the protocol from Zuur et al. (2009) was performed in R, using the packages "stats" (standard R package), "nlme" (Pinheiro et al. 2009) and "multcomp" for multiple comparisons (Hothorn et al. 2008). For each part of the data, we started with a full general linear model, considering all fixed effects and their interactions. A random structure was then chosen, comparing different models – with the same fixed effect structure - using ANOVA (log-likelihood ratio test) and Akaike's Information Criterion (AIC). The different random structures tried included day of measurement and individual ants (nested in "day") as effects. Once the random structure was chosen, the fixed effects with no significant effect were removed one by one. AIC was computed for each model, and the model with lowest AIC was chosen as best minimal model. To validate the final model, residuals were observed to check for non-randomness and deviations from a normal distribution.

Results

Overall, no significant effect of worker type was found in the response to the different stimuli. The data set comprised 16 nurses and 15 foragers (one forager was irresponsive to most stimuli and was therefore considered an outlier).

For the data including the response to larval CHC and its control, pentane (Figure 6.2), the best minimal model included only individual ants as a random effect. Both worker type and stimulus type had non-significant effects and could be eliminated from the model, which means that the antennal response to larval CHC extracts is not significantly different from the response to the control.

For the data of response to 1-octanol solution and its control, mineral oil, the best minimal model included only stimulus as fixed effect. Adding a random structure did not significantly improve the model. Once again, worker type had no significant effect (Figure 6.3). To account for some heterogeneity of variances between the two different stimuli, we allowed a different variance parameter to be estimated for each stimulus group. The response to 1-octanol was significantly larger than the response to the control (coefficient=3.77, t-value=12.33, df=60, $p<10^{-4}$).

As for the adult CHC extracts data, the best minimal model included stimulus as a fixed effect and random slope and intercept per individual ant. Again, no significant difference existed in the response to stimuli between different worker types. The response to non-nestmate CHC extract was significantly stronger than the response to nestmate CHC extract (Figure 6.4), as shown by a post-hoc comparison using Tukey contrasts (estimate=2.06, z-value=12.27, $p<1\times10^{-6}$). Both responses to nestmate and non-nestmate CHC were significantly higher than the response to the solvent (solvent – nestmate CHC: estimate=−0.74, z-value=−4.75, $p=3.6\times10^{-6}$; solvent – non-nestmate CHC: estimate=2.8, z- value=−12.96, $p<1\times10^{-6}$).

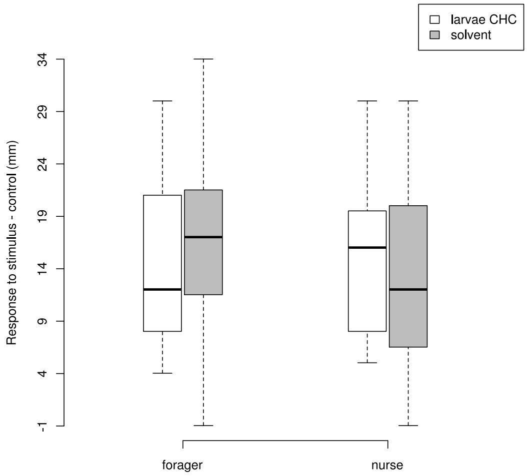

Figure 6.2: Box-whiskers plot (first quantile, median and fourth quantile indicated by the box, whiskers indicate minimum and maximum range of values) of the antennal response in cm to larval CHC extract and pentane (total response minus the corresponding antenna's response to air) of foragers (white boxes) and nurses (grey boxes).

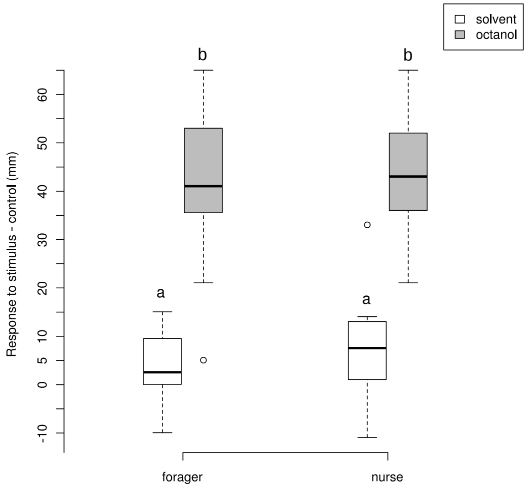

Figure 6.3: Box-whiskers plot of the antennal response in cm to 1-octanol (%) and its solvent, mineral oil, (total response minus the corresponding antenna's response to air) of foragers (white boxes) and nurses (grey boxes). Significantly different groups are indicated by different letters above the boxes. White circles indicate outliers.

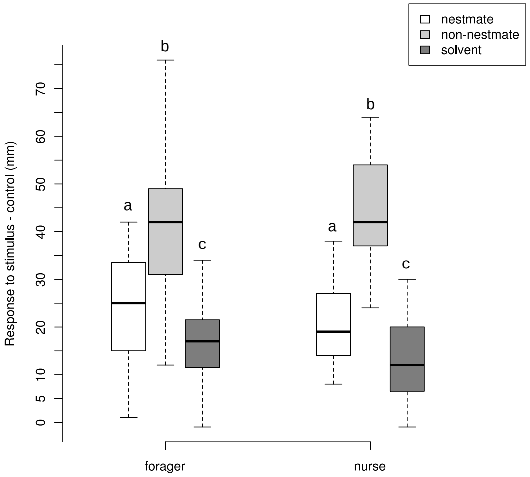

Figure 6.4: Box-whiskers plot of the antennal response in cm to nestmate CHC extract, non- nestmate CHC extract and solvent (total response minus the corresponding antenna's response to air) of foragers (white boxes) and nurses (grey boxes). Significantly different groups are indicated by different letters above boxes.

Nurses tended to show a larger response than foragers to the mechanical stimulus (air) (Figure 6.5). This tendency is marginally significant (coefficient=0.8, *t*-value= 2.02, df=31, p=0.052).

Discussion

Overall, no significant difference was found between nurses and foragers in the response to chemical stimuli. This might indicate that the behavioral differences between these workers are derived from processes not related to antennal detection of stimuli, but taking place in the central nervous system. An alternative explanation for the results obtained is that the workers collected were not in fact specialized in different tasks, and hence did not differ in their response to stimuli. Our classification of individuals as "nurses" and "foragers" was based on observations that workers of *C. fellah* do perform the same tasks at least over the course of a week (A. Duarte, unpublished data). However, these observations had a small sample size and therefore would need to be verified with further behavioral observations to establish a clearer relationship between task choice and EAG response.

Nevertheless, nurses and foragers did differ, though only marginally, in their response to the mechanical stimulus (air). The fact that the nurses' antennae tended to

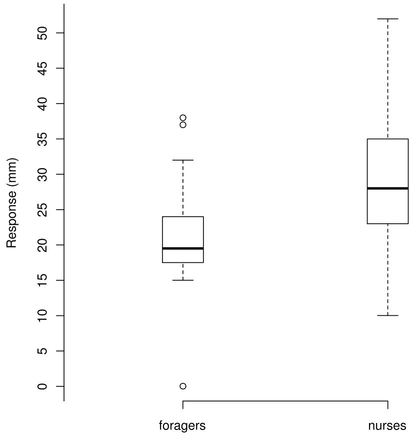

Figure 6.5: Box-whiskers plot of the antennal response to mechanical stimulus (air) from foragers and nurses. The difference between nurses and foragers is marginally significant.

show stronger responses to the mechanical stimulus suggests an intrinsic difference between the two groups of workers, which could be related to the environment to which they are habituated. The workers identified as nurses were collected in the nest area, which is constantly covered with a dark lid. The foraging area, where workers classified as foragers were collected, is exposed to the air. Nurses may therefore be more sensitive to stimulation with air flow, something to which they are not usually exposed. There may be a habituation factor that leads to foragers being less sensitive to air flow. Another potential factor behind the difference between nurses and foragers, is that, in most species of ants, nurses are also the younger individuals in the colony (Oster & Wilson 1978, Hölldobler & Wilson 1990). Therefore there could also be a senescence effect that causes foragers to be less sensitive to air flow. However, one might expect such senescence to affect also chemical receptors, which would mean that foragers should respond in a weaker way to chemical stimuli. This is not what we observe for the chemical stimuli presented (CHC extracts, 1-octanol and solvents).

The stimulus used as being associated with food (1-octanol) elicited a significantly higher response than its control. The focal colony had been previously conditioned to associate the odor of 1-octanol with food. However, there is the possibility that this habituation had waned at the time the EAG measurements were taken. It could also simply be that for the workers 1-octanol was a general odor that elicited a strong response (Brandstaetter et al. 2011), with no particular association with food.

The response to larval CHC was not significantly different from the response to the control (pentane). This may indicate that larvae are not recognized through their CHC composition. Other chemical cues may be involved, as well as visual cues. Alternatively, it is possible that the concentration of the larval CHC extract was too low to be detected by the antennae. However, care had to be taken not to deplete the colony's brood, since this colony will be used in the future for other studies. To understand why larval CHC are seemingly not detected by the antennae, it would be useful to perform gas-chromatography on the larval CHC extract to obtain the cuticular profile of *C. fellah* larvae. In other ant species, evidence suggests that the CHC profile of larvae is similar to that of workers. For example, in *Myrmica* ants, the cuticular profile of larvae has been shown to not differ from the CHC profile of workers (Elmes et al. 2002). In *Oecophylla smaragdina*, larval CHC profiles differ between colonies; evidence suggests that the consumption of *O. smaragdina* larvae of the host colony by the myrmecophilous spider *Cosmophasis bitaeniata* provides the spider with a "nestmate-like" CHC profile, thus avoiding attack by ant workers (Elgar & Allan 2004).

An alternative explanation for the lack of detection of larval CHC's by worker antennae is that antennae detect odors which are alien to the colony, with workers being functionally anosmic to colony odors, perhaps owing to desensitization of receptor neurons to these odors or to habituation (Guerrieri et al. 2009, van Zweden & d'Ettorre 2010). This explanation, however, is not entirely in accord with the results obtained with nestmate CHC's. The response of antennae to nestmate CHC's was significantly higher than the control, albeit much smaller than the response to non-nestmate CHC's, suggesting that both nestmates and non-nestmates are detected. To control for this hypothesis though, it would be interesting to do EAG tests for non-nestmate larval CHC's.

The choice of exposing workers to nestmate and non-nestmate CHC odors was made to test for any differences between foragers and nurses in their reaction to stimuli related to nest defense. However, our results contribute also to the ongoing debate on nestmate recognition systems. The fact that the response of the antennae was higher towards non- nestmate CHC's suggests a recognition system where alien chemical compounds elicit a stronger response than the colony's own compounds. Ozaki et al. (2005)described a chemosensory sensillum in the antennae of *C. japonicus* that responds only to non-nestmate CHC blends, supporting the hypothesis of a non-nestmate recognition system. Brandstaetter et al. (2011), however, found that both nestmate and non-nestmate colony odors elicit neuronal activity in the brain of *C. floridanus* workers. It is not clear whether there is a difference between neuronal activity patterns elicited by nestmate and non-nestmate odors.

It would be of extreme importance to repeat these tests in more *C. fellah* colonies, but also in other *Camponotus* species. In *C. fellah*, workers react aggressively to individuals whose CHC profile diverges from the colony's CHC profile (Boulay et al. 2004). In *C. herculeanus*, it was found that aggressive behavior was induced by exposing individuals to particular alien cuticular hydrocarbons (Guerrieri et al. 2009), but not by the lack of one of the colony's own hydrocarbons. It would be interesting to test if a similar pattern in EAG response would occur in this species. Guerrieri et al.'s findings, like Ozaki et al.'s (2005), suggest a recognition system based on the recognition of alien compounds, instead of a "template label-matching" system (e.g., Crozier & Dix 1979). Our data suggests that in *C. fellah* workers' antennae can detect nestmate CHC blends as well. Perhaps the particular olfactory receptors activated are of importance to determine the subsequent behavioral reaction. Nevertheless, the difference between the response to nestmate CHC and solvent is quite small, when compared to the large difference between non-nestmate CHC and solvent. Furthermore, the nestmates used to prepare CHC extracts were taken from the foraging arena. It is possible that the CHC profile of foragers, being exposed to outside influences, differs slightly from the colony gestalt odor. It would be interesting to test the EAG response of workers to "nurse" nestmates. Hence, we cannot dismiss a system based on recognition of alien compounds in *C. fellah*, as habituation to the colony odor – which could cause the lower antennal response relative to the response to non-nestmate odor – may still play an important role in the behavioral reaction of workers to nestmates. In *C. aethiops*, for example, repeated exposure of antennae of live tethered ants to non-nestmate odors results in a decrease of the aggressive response (measured using standard aggression tests) (Stroeymeyt et al. 2010). On a more general note, there may potentially be a diversity of recognition systems across related ant species. The study of different recognition systems in ants may provide important insights in the evolution of signaling systems under different ecological circumstances.

The present study serves as a pilot which aimed to compare different "specialist" workers in their reaction to particular task stimuli. Our results do not support differences in reaction to chemical stimuli among task "specialists", but emphasize a potential role of desensitization to stimuli in creating behavioral differences. The results presented here should be complemented with behavioral observations and gas-chromatography of the CHC samples, to obtain CHC profiles for workers of different types and larvae.

Acknowledgements

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Chapter 7

Synthesis

Ana Duarte

Evolutionary theory typically addresses the evolution of behavior from an optimality perspective, often assuming that adaptive behavior will evolve, regardless of the underlying behavioral mechanisms. Recently, the role of behavioral mechanisms and decision rules has gained more attention, and researchers have been urged to consider these explicitly when modeling the evolution of behavioral traits (McNamara & Houston 2009, Fawcett et al. in press). The work presented in this thesis has strong parallels with the recent views on adaptive behavior, but interestingly it was sparked by the opposite problem: theory on division of labor has placed much emphasis on behavioral mechanisms and decision rules potentially underlying division of labor, in the form of self-organization models, but neglected to consider the role of evolution in shaping these mechanisms (Duarte et al. 2011).

The importance given to self-organization is nevertheless justified. Self-organization occurs widely in nature and explains how seemingly simple organisms can display intricate group-level patterns (Camazine et al. 2001). For example, spiral waves in *Dictyostelium discoideum* aggregates (Sawai et al. 2005), pheromone trails in ants (Bonabeau et al. 1997), and mussel bed patterns (de Jager et al. 2011) can be explained by self-organization. Social insect workers show a relatively high degree of behavioral specialization, which is likely also a result of self-organization. Nevertheless, natural selection may hone the behavioral rules underlying self-organization, favoring those that produce the most adaptive emergent patterns of division of labor. There was a need for models that integrate self- organization and evolution in the context of division of labor.

In chapter 2 I suggest a general approach to the integration of self-organization and evolution. This approach considers two different time-scales (see Figure 2.2). At an ecological time-scale, a group of individuals interacts with the environment and with each other, making behavioral decisions based on genetically encoded behavioral rules. Division of labor may emerge during this period. The productivity of the group results from the individuals' behavioral decisions. At an evolutionary time-scale, productivity is translated into fitness. Groups will differ in the fitness accrued. Natural selection then acts to favor those behavioral rules which produce adaptive group-level outcomes. Behavioral rules, or the parameter values underlying these rules, may change as a result of mutation and natural selection. In chapters 3 and 4, I implemented this unifying approach, taking two well-known self- organization models as point of departure, namely the fixed threshold model (Bonabeau et al. 1996) and the reinforced threshold model (Theraulaz et al. 1998). In chapter 5, I allowed for the behavioral rules underlying individual behavior to be more flexible, implementing simple artificial neural networks, and I examined the effect of different behavioral architectures on the evolution of division of labor. I will first summarize the main insights obtained from the theoretical models developed, and make a critical assessment of the limitations of these models, in the light of the benchmarks suggested in chapter 2. I will then discuss future avenues of research, both theoretical and empirical.

Main insights from integration of evolution and self- organization

In chapter 3 I examine the evolution of response thresholds in a population where individuals are grouped in colonies. During a work phase, individuals have to perform two tasks. For each task there is an associated stimulus level which can be interpreted as an environmental signal of task need. Task stimulus grows in the absence of work, and decreases when work is performed. Individuals perform a task whenever the task stimulus surpasses their threshold for that task. At the end of a work phase, colonies produce offspring in proportion to their accrued fitness, which is a function of how much had been done during the work phase and of the proportion of work allocated to each task. The populations started out with identical thresholds. Thresholds are inherited and allowed to mutate at a certain rate. Under these circumstances, the thresholds converge to zero and no division of labor occurs, because all individuals evolve very similar, low thresholds. This result, at first sight unexpected, is easily understood: lowering the thresholds allows individuals to be active at lower stimulus values, thus minimizing the number of time steps where individuals are idle. When we consider a situation where division of labor would be adaptive, by adding a time cost when workers switch tasks, then a very different outcome is obtained. Under switching costs, the populations go through evolutionary branching (Geritz et al. 1998), and become polymorphic for both thresholds. When branching occurs, division of labor is possible; colonies that have individuals with different thresholds, some having lower thresholds for one task, others having lower thresholds for the other task, show worker specialization and division of labor. However, some colonies possess individuals with very similar thresholds, and those colonies do not achieve division of labor. Hence, while it is possible to evolve division of labor in the response threshold model, the division of labor obtained is highly dependent on the exact genetic composition of the colony. To allow division of labor in all colonies in the population, one would have to consider a process that increases the chance that individuals with different thresholds form a colony, such as disassortative mating. Intuitively, it would seem also logical to assume that multiple mating would have a beneficial effect on the evolution of division of labor, because it increases within-colony genetic diversity. However, we observed that multiple mating does not facilitate evolutionary branching of thresholds, because the beneficial effect of rare mutations is diluted when foundresses mate with several males.

I have also looked at the fine-tuning of division of labor to particular colony needs in terms of the proportion of work allocated to each task. It is reasonable to assume that different tasks may require different numbers of workers devoted to them (Gordon 1996). In self- organization models, whenever asymmetries among task needs are considered, it is assumed that the individuals aptly recognize this from the environmental cues available. Hence, individuals are assumed to behave adaptively, even if it is unclear how they have come to possess such information. However, I argue that the individuals' perception of task need should evolve; in a scenario where, to maximize fitness, one task should be performed more often than another, the behavioral rules should evolve to produce such an outcome. In chapter 3, I show that in the current implementation of the response threshold model, it is not possible to obtain an asymmetric work distribution through the evolution of thresholds alone, even under strong selection on work distribution. This is a major limitation of this model, which is maintained in the reinforced threshold model (chapter 4).

In chapter 4 I study the reinforced threshold model (Theraulaz et al. 1998, Gautrais et al. 2002), keeping the same basic model structure as in chapter 3. The main difference between the models is that the response threshold, instead of being fixed throughout the lifetime of an individual, may change with experience, decreasing when a task is performed and increasing when it is not. Here I allow the reinforcement parameters to evolve, starting from a homogenous population with no reinforcement. I examined three different scenarios: First, division of labor brings no selective advantage; second, switching tasks is costly in terms of time (as in chapter 3); third, the efficiency with which individuals perform a task increases with experience. Hence scenarios 2 and 3 portray different situations in which worker specialization (and division of labor) may be adaptive. Interestingly, we observed already in scenario 1 that some degree of division of labor evolves. Selection for minimizing idleness favors colonies with high positive reinforcement (where thresholds decline after task performance), an outcome that parallels the evolution of thresholds to zero in the fixed- threshold model (chapter 3). However, in contrast to the fixed-threshold model, reinforcement leads to an effect of early experience in the differentiation of thresholds, resulting in specialization in some individuals. Division of labor thus evolves as a mere by-product of selection for minimizing idleness. This result illustrates that considering specific behavioral mechanisms is of great importance when modeling the evolution of behavior. The inclusion of switching costs in the reinforced threshold model (scenario 2) leads to the evolution of division of labor via the co-evolution of positive and negative reinforcement, whereas considering an increase of efficiency with experience (scenario 3) also leads to division of labor but only through the evolution of negative reinforcement. These different outcomes reflect the priorities imposed on colonies in the different scenarios: In scenarios 1 and 2, the priority is to reduce idleness, for which the evolution of positive reinforcement is required, whereas in scenario 3 the priority is to increase the efficiency of individuals, by sticking to tasks that are familiar. Therefore, only evolution of negative reinforcement is required. In scenario 3 I examined also the effect of the probability to remember past experience on the evolution of division of labor. When individuals could easily remember their past experiences, division of labor did not evolve. Under these circumstances, specialization brought no advantage because individuals were able to maximize the efficiency of task performance for both tasks by switching among them.

In chapter 5, I implement artificial neural networks and allow the connection weights of the networks to evolve. I also study different types of network architecture. A major insight from this model is that the type of architecture considered is of great importance for the evolutionary outcome. Feedforward and recurrent networks were both considered in the model (Haykin 1999). Feedforward networks allow for the evolution of division of labor in the presence of switching costs, but the level of division of labor obtained is dependent on the specific genetic composition of the colony, as in the fixed response threshold model. Similar to the threshold model, the feedforward network model is limited in the extent to which worker distribution can be fine-tuned to task needs. Recurrent networks, however, allow for a more flexible distribution of workers, almost perfectly adapted to the colony needs. Owing to the flexible behavior of individuals, the patterning of genetic variation does not constrain the level of division of labor that can be achieved in the course of evolution. In light of chapters 3, 4 and 5, it can be concluded that behavioral mechanisms allowing for a feedback of individual experience on the tendency to perform tasks leads to more robust division of labor than mechanisms requiring genetic task determination.

Robustness of current models

In this thesis I focused mainly on differences between behavioral architectures. Several assumptions were kept constant, often making use of assumptions previously made in the literature, for simplicity and comparison between models. In this section I will discuss the robustness of the models presented in this thesis. First, this will be addressed in light of the benchmarks suggested in chapter 2 for evolved mechanisms underlying division of labor. I will then discuss some assumptions of the current models and how altering these assumptions may change their outcome. For this purpose I will make use of recent results obtained in a more realistic version of the models presented in chapters 3 to 5.

Benchmarks of an evolved mechanism for division of labor

Evolved mechanisms underlying division of labor should possess the following benchmarks (Duarte et al. 2011):

- emergent specialization
- adaptive distribution of workers
- flexibility
- developmental robustness

- evolutionary attainability and stability

Emergent specialization, i.e., specialization that arises through the interaction between individuals and their environment, was obtained through the evolution of all the different behavioral mechanisms studied, although with limitations. An adaptive distribution of workers was not achieved with most mechanisms; it was only obtained by the evolution of recurrent neural networks (chapter 5). Even then, when worker specialization and asymmetric worker distributions had to evolve together, the behavioral mechanism could not produce a perfectly adapted response. It is unclear whether this is owing to a limitation of the behavioral mechanism or to other assumptions in the model, such as those on the stimulus dynamics or on the fitness function.

The flexibility of evolved mechanisms for division of labor should allow for groups of individuals to cope with environmental changes that require an adjustment of the number of workers performing each task (Duarte et al. 2011). This has not been properly tested in the models presented in this thesis. It would be easy to extend these models to test for the ability of colonies to respond to environmental fluctuations. In the classic fixed threshold model, a sudden increase in task need results in an increase in the number of workers performing the task (Bonabeau et al. 1996). Hence, the threshold mechanism has the potential to respond flexibly to environmental fluctuations. Nevertheless, the evolution of worker specialization may be hampered by the existence of frequent environmental fluctuations. The benefits of specialization (e.g., avoiding time costs, increasing work efficiency) and the costs of behavioral rigidity in a situation in which the environment varies must be taken into account in the same framework.

The developmental robustness of evolved mechanisms for division of labor means that colonies should be able to cope with task requirements regardless of their internal state. Within-colony genetic variability, colony demographic structure, or the developmental dynamics of the colony should not interfere with the colony's ability to respond adaptively to the environment. In the current models, I found that recurrent neural networks were the most robust mechanism (chapter 5), not requiring specific patterns of genetic variation to produce division of labor. The robustness of evolved mechanisms for division of labor to the colony's demographic structure and developmental dynamics was not yet properly tested. All the models considered thus far have assumed a constant colony size, but a more mechanistic approach would include a limited lifespan of workers and changes in colony size throughout the life of a colony.

Evolutionary attainability and stability are also benchmarks of an evolved mechanism for division of labor. These are particularly important because potentially several mechanisms exist that can produce division of labor, but not all are evolvable or able to resist invasion by other mechanisms. Evolutionary stability is addressed in the models presented here by allowing for mutations to constantly trickle in the population. The behavioral strategies that are not destabilized by the incoming of new mutations can be considered equilibria in the simulations. In chapter 3, the threshold mechanism is not stable (i.e., all thresholds evolve to zero) when there are no costs to switching. When there are costs to switching, the threshold mechanism becomes stable. In chapter 5, genetic task determination is stable in the feedforward neural network model, but not in the recurrent neural network model.

Another aspect of the evolutionary stability of mechanisms for division of labor has to do with levels of selection. So far, models of division of labor have only considered colony- level selection. Model outcomes could change drastically if different levels of selection are considered. It is well known that conflict may occur within social insect societies between workers and queens (Bourke & Franks 1995), and this may decrease the benefits accrued with division of labor (but see Franks et al. 1990). If selection favors worker reproduction, this may negatively impact on division of labor, leading to more workers being idle.

Assumptions of current models

Simplicity of behavioral architectures

In the models presented in this thesis I have considered only very simple behavioral architectures. It can be argued that the limitations encountered in neural network models are partly owing to the simplicity of the networks, and that therefore more complex networks should be considered. Future models using artificial neural networks could include the evolution of network topology, as well as connection weights, thereby allowing the evolution of new nodes and more complex architectures. However, modeling more complex networks will come at a cost. As the number of nodes and connection weights increases, tracking the evolution of more complex networks becomes more difficult. Establishing clear causal relationships between the parameters of the network and individual behavior may also be less feasible. Therefore extracting relevant conclusions from the evolution of such complex networks may be difficult.

Task demand and nature of tasks

Several unrealistic assumptions concerning the nature of tasks and stimulus dynamics were made in the models presented here. An important assumption is that there is equal increase in stimulus for both tasks. However, it may be that for some tasks, stimulus increases at a higher rate. In the response threshold models, stimulus dynamics determines worker distribution to a large extent (chapter 3), thus asymmetries in stimulus increase could alter the outcome. For example, if the asymmetry in stimulus increase would be in the same direction as the asymmetry in the relevance of tasks for fitness, colonies could be able to reach the optimal work distribution.

Another important assumption made is that the stimulus increase is constant over the lifetime of a colony. However, the demand for tasks may change over that period (Oster & Wilson 1978). Nest construction, for example, may be more necessary in the initial stages of colony development, whereas brood care may increase in demand with time. Changes in task demand may make specialization more difficult to evolve because individuals would be required to switch tasks at certain moments.

Tasks were considered to be independent. The stimulus existing for one task did not directly affect the stimulus for the other task. In reality, tasks may be interconnected, such that the performance of one task allows the performance of another task. An example of this is found in nest construction in paper wasps, where there is a delicate balance between foraging for different materials which are combined to form the nest walls (Jeanne 1986b, 1996). Even without considering more complex tasks such as nest building, we can find plausible situations in which tasks would be interconnected. Focusing only on the general tasks of foraging and brood care, it can be argued that the successful performance of brood care depends on the amount of food that has been collected by the foragers. This could potentially have an effect on the evolution of division of labor, as the need to assure that foraging is constantly being performed could create an advantage to worker specialization.

One of the most crucial assumptions made concerns the relationship between task performance and fitness. In the fitness functions used throughout this thesis, task performance always accrued fitness. However, tasks can also be of a homeostatic nature, that is, fitness is gained only when task stimulus is maintained within certain bounds. An example of such homeostatic tasks is the maintenance of nest temperature in honey bees and bumble bees (O'Donnell & Foster 2001, Weidenmüller 2004). Evolution of response thresholds for a homeostatic and a maximizing task (where stimulus should be removed as much as possible) was considered in a theoretical study by Tarapore et al. (2009). Unfortunately, the authors do not report how worker specialization was affected. However, in such a situation there is a pressure for ensuring that the homogeneous task is kept within bounds, which may lead to the evolution of a specialized worker caste.

Fitness function

Considering more realistic approaches to task nature and stimulus dynamics is important because ultimately these factors define fitness in real life insect colonies. In the models presented in this thesis I assume that fitness increases linearly with the amount of work performed, and that tasks are optimally performed in a certain proportion. Some of the results obtained may not hold under different fitness functions. For example, the result obtained in chapter 3, in which thresholds evolve to zero under the assumption that switching is not costly, would not hold if there would be no selective pressure to maximize the amount of work done. In fact, when the fitness function places more emphasis on the component of work distribution, we see that thresholds do not always evolve towards zero.

In real insect colonies, fitness is determined by the number of reproductive individuals that a colony produces. The number of reproductives produced may depend on the tasks performed in different ways. It may increase linearly with the performance of certain tasks (such as brood care), but it may also depend non-linearly on the performance of other tasks, such as nest-maintenance. It would be important to test different fitness functions that make more realistic assumptions on the relationship between task performance and fitness.

Towards a more realistic model of evolved division of labor

As argued above, the assumptions made in current models on fitness and stimulus dynamics are far from realistic. In order to explore how a more realistic model could look like, we developed a model in which stimuli receive a more concrete interpretation and in which fitness is more directly related to the reproductive output of a colony (A. Duarte, O. Ivanov and F. J. Weissing, in preparation). In this model, we consider again two tasks, now specifically interpreted as foraging and brood care. Performance of foraging increases the level of food stored in the colony, whereas performance of brood care increases brood condition. In contrast to the earlier models, we explicitly consider a link between the performance of the two tasks: when a worker performs brood care, the level of food stored in the colony is decreased by a certain amount, mimicking food consumption by larvae. Similarly, every time step workers consume some of the food stored owing to energetic costs. Brood condition declines also at a certain rate. To choose between tasks, individuals assess the level of food in the colony and the current brood condition. These variables are transformed so that stimulus is higher when the level of food stored or brood condition is lower. Individual decisions are governed by a neural network, similar to the feed-forward neural networks in chapter 5. The connection weights of these networks were allowed to evolve. However, in this first attempt at a more mechanistic model for division of labor, sexual reproduction was excluded for simplicity. Colonies are founded by one individual and workers are all clones of this individual.

With this basic model, we consider three different scenarios in terms of fitness function. These scenarios were designed as steps building up from our previous fitness function towards a more realistic one. In the first scenario, fitness is the product of the amount of stored food and the level of brood condition at the last time step of the simulation. We will refer to this fitness function as “final productivity”. The assumption is that more reproductive individuals can be produced if the level of stored food is high and the brood is well-fed. However, it can be argued that the activity of the workers throughout the lifetime of the colony is relevant for fitness. The second scenario thus considers fitness to be a function of the product of food stored and brood condition as well, but now this product is summed over the time steps of the working phase. Hence, in this scenario it is important that the two tasks are maximized during the colony’s lifetime. We will therefore refer to this scenario as “colony lifetime productivity”. The third and last scenario envisages a more realistic approximation of fitness: fitness de-

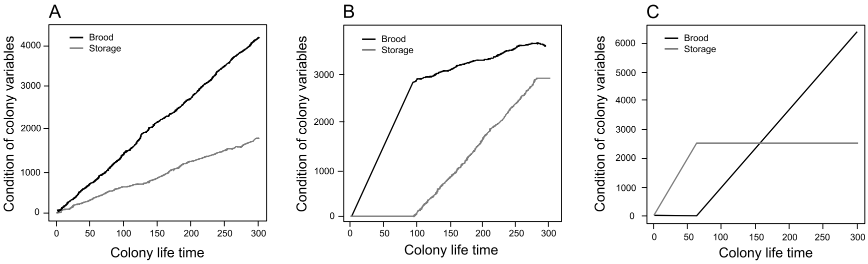

Figure 7.1: In a more realistic model for evolution of division of labor, we explicitly consider foraging and brood care as the two main tasks performed by the colony. Stimulus dynamics is replaced by the dynamics of stored food and brood condition. This figure illustrates the importance for the colonies' evolved behavior of how fitness is affected by food storage and brood condition. We show a representative colony in each panel. A) fitness is determined by final productivity. Workers perform the two tasks equally, resulting in lower levels of food storage because of the higher consumption rate. B) fitness is determined by the colony's lifetime productivity. Individuals now spend the initial time steps accumulating food in the storage, so that the productivity over the lifetime of the colony can be C increased. C) fitness is determined by the acquired brood condition(with brood care being dependent over the simulation on the level of food stored). Individuals also evolve to perform exclusively foraging in the initial time steps, so that brood care efficiency can be maximized in the following time steps.

pends on the end level of brood condition only. However, during the work phase, the efficiency of brood care (i.e., the increase in brood condition caused by performance of brood care) increases with the amount of food in storage, with diminishing returns. Hence, with a low level of food stored, workers are not able to improve brood condition. This again puts pressure on workers to perform the two tasks in parallel. We will refer to this fitness scenario as "acquired brood condition".

The third fitness function scenario is the closest to a more mechanistic approximation of fitness that we have considered so far. Annual colonies of social insects, for example, typically increase only the number of workers during the year, and then raise reproductive individuals during the summer (Wilson 1971). Only the last batch of brood is actually important for the queen's fitness; the success of the brood, however, depends on how many workers are available for foraging and nursing.

The rate of food consumption was set to be to twice as large as the rate of decrement of brood condition. When fitness is determined by final productivity, foraging and brood care are performed equally during the work phase, with the result that the storage level increases at a slower rate than the brood condition (Figure 7.1A). However, when fitness is determined by colony lifetime productivity, a strategy is chosen in which food is accumulated in the initial time steps, switching later to a mixed per-

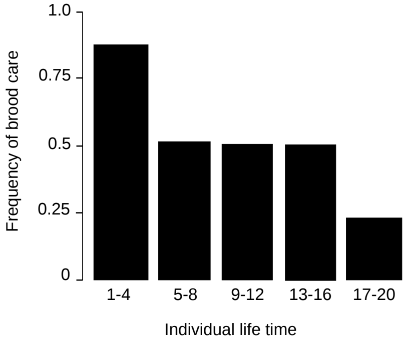

Figure 7.2: Model in which colony demographics is considered, alongside an explicit treatment of the dynamics of food storage and brood condition. Fitness is determined solely by the acquired brood condition. Foraging entails an additional risk to the baseline mortality. Under these conditions we obtain division of labor via age polyethism: young individuals perform brood care more frequently, and old individuals forage more frequently. Average frequency of brood care across individuals in each age classe is shown for a representative colony.

formance of brood care and foraging (Figure 7.1B). This allows colonies to maximize brood condition and food storage over a period of time steps. When fitness is determined by acquired brood condition, individuals also evolve to exclusively forage in the first time steps, bringing the level of food storage up to where brood are efficiency becomes maximal. The remaining time steps are mostly devoted to brood care, with foraging being performed sporadically (Figure 7.1C). Note that none of these outcomes represent division of labor because all individuals follow the temporal changes in task preference. Hence, at any specific time step, the large majority of individuals are performing the same task. Nevertheless, these results reveal how different fitness functions can drastically affect the evolution of behavioral strategies.

Division of labor evolves in this model when we consider the dynamics of colony demography. We assume that workers have a baseline mortality, and may suffer higher mortality when foraging. In brief, our results indicate that in cases in which the extra mortality associated with foraging is substantial, age polyethism evolves, where young workers mostly nurse the brood, and older workers forage (Figure 7.2). This result is in accordance with previous theory on social insects (Jeanne 1986a, Wakano et al. 1998), which argues that avoiding risky tasks at younger ages (when survival probability is high) allows higher colony productivity.

Future research avenues

Spatial structure

In the models considered in this thesis I do not explicitly consider a spatial structure of the nest. However, in real colonies, tasks are often spatially distributed. The effect of the spatial distribution of tasks and associated stimulus on worker behavior has been emphasized in a few self-organization models (Tofts 1993, Johnson 2009, 2010, Richardson et al. 2011). In my models, I have only implicitly considered space, when I assumed there could costs to switching tasks which could derive from traveling between task locations.

One of the consequences of considering space is that it forces modelers to formulate more precisely how individuals acquire information on task stimulus, namely how they move in the environment. In response threshold models, for example, it is often assumed that individuals and stimuli are well mixed, and hence individuals have all the information required for decision-making at their disposal. It is not specified how exactly individuals acquire this information, and admittedly this is not the scope of such models. The explicit treatment of space allows us to consider other behavioral rules that may lead to division of labor. For example, individuals can move in different types of random walks, or at different speeds, or simply with different probabilities, some tending to stay in the same location more than others. It follows from this that individuals may gather different information about task stimuli, which could lead to behavioral differentiation. It would be particularly interesting to investigate how different distributions of tasks in space would affect the evolution of movement rules and division of labor.

Phenotypic plasticity

Another important avenue of research would be to consider the evolution of developmental pathways that could provide behavioral differentiation between workers via phenotypic plasticity. This would allow for division of labor even in the absence of genetic polymorphism.

Typically, phenotypic plasticity in social insects is considered when discussing morphological castes or differentiation between worker and reproductive castes. However, it has been shown that developmental circumstances can also affect behavioral thresholds. Weidenmüller and coworkers (2009) found that in workers of *Camponotus rufipes* the temperature during the pupal stage affected their temperature threshold for removing brood from heated locations. Workers that had experienced low temperatures as pupae, started to move the brood at lower temperatures than workers that had experienced high temperatures during the pupal stage. Perhaps other factors during development (e.g., humidity, amount of brood care received) can influence other behavioral thresholds, thus contributing to behavioral differentiation.

Importantly, an effect of early developmental circumstances on behavioral preferences may have other adaptive functions, besides being a source of phenotypic variation. For example, if the environment during the development of workers is representative of the environment of the brood to which workers will tend, a plastic response may allow the colony to track environmental changes occurring at a slow enough rate. In the study of Weidenmüller et al. (2009), workers raised at high temperatures, although being apparently less sensitive to heat, transported the brood to places at lower temperatures than workers raised at low temperatures. This could be adaptive during summer months, when temperatures rise quickly during the day. Placing brood in the cooler locations of the nest would avoid having to move the brood very frequently. It would be interesting to develop models studying the evolution of phenotypic plasticity of behavioral thresholds and its effect in division of labor. It would be particularly important to include environmental fluctuations in such a model.

Division of labor and the evolution of sociality

The implicit assumption of the models presented here is that the evolution of eusociality (i.e., reproductive division of labor) preceded the evolution of worker specialization in different tasks, as we consider colonies with sterile workers and not solitary individuals. This assumption probably applies to the evolution of morphological specialization, where the exaggerated structures evolved by workers of certain morphological castes would be detrimental for individuals able to gain direct fitness. A comparative analysis of taxa showing division of labor (Simpson 2012) suggests indeed that evolution of reproductive division of labor has either preceded or co-occurred the evolution of other types of division of labor, such as the evolution of morphological castes. However, in terms of behavioral specialization, which is unlikely to be captured in the fossil record, it is not clear whether the evolution of eusociality is a pre-requisite. Some insights can be taken from allodapine bees, a group showing large variation in degree of sociality from subsocial to eusocial. Schwarz et al. (2010) argue that allodapine bees use different behavioral strategies depending on whether they have a reproductive position or not. While reproductive individuals are forced to forage in order to feed their larvae, new females that have not yet attained a reproductive position can better avoid the risks of foraging and stay and "wait" at the nest. While waiting, these individuals take on other roles inside the nest, and thus an incipient form of division of labor arises between foragers and nest-workers.

In this ancestral form of sociality hypothesized by Schwarz and colleagues, where sterile castes are not yet envisaged, division of labor may merely be the consequence of the necessity of queuing at the natal nest, due to ecological factors such as scarcity of nest sites. If this hypothesis is correct, division of labor precedes eusociality in allodapine bees. The authors further hypothesize that eusociality could evolve due to extreme ecological constraints that would limit direct fitness benefits of queuing individuals, thus leading individuals to invest in indirect fitness.

The role of division of labor in the transition to eusociality may have also been important. The mere presence of individuals at the nest, while others go foraging, may decrease the risk that the brood is attacked by predators. Nest-guarding, and the parallel performance of other tasks, could greatly increase indirect fitness, and thus facilitate the evolution of eusociality. It would be interesting to develop a model where division of labor and eusociality could evolve, for example considering that individuals may choose between delaying reproduction, staying at the natal nest, or leaving to found their own nest. At the natal nest, individuals could choose to work on a set of different tasks or remain idle, a decision which would have an impact in the success of the brood. The evolution of these behavioral decisions could be tracked under different ecological contexts, where the probability to find suitable nest sites or food sources would be varied. I predict that given more rigorous environmental conditions, the probability to delay reproduction would increase, and so would the probability to work at the natal nest. Such a scenario could be modeled using different approaches. Analytical techniques such as game theory and inclusive fitness theory could be employed, and for a more mechanism-based approach, individual based simulations with behavioral decisions being governed by a neural network could be used. It would be interesting to observe what the outcome would be for the different techniques.

Empirical research

It is still poorly understood how individuals perceive stimulus, and how change in stimulus affects task choice. In chapter 6, I presented a pilot study on the ant *Camponotus fellah* where a simple electrophysiological technique was used to test whether the antennae of different types of workers have different abilities to detect chemical stimuli. The conclusion from this study was that no difference could be observed between the two types of workers assessed (nurses and foragers) in the way their antennae perceived chemical stimuli. Nevertheless, I did find a tendency for nurse-antennae to respond more strongly to a mechanical stimulus (exposure to air flow). This indicates that foragers may have lost sensitivity to mechanical stimuli, whereas nurses, being typically inside the nest, are less exposed to air currents and are therefore more sensitive to it. Another puzzling aspect of this study was that the antennae of both nurses and foragers were seemingly unable to detect the cuticular hydrocarbons of larvae. Further work on this species should be done to understand whether this was due to a protocol error or if this result is evidence that detection of larvae in *C. fellah* occurs through other signals. More work is required to deepen our knowledge on potential differences between workers in stimulus perception.

The adaptive reasons behind worker specialization are still poorly understood. So far, to my knowledge, only one study explicitly addressed this question. This study did not find any correlation between worker specialization and individual task efficiency (Dornhaus 2008). There may be several reasons for this result. On the one hand, individual efficiency was measured in contexts where stimulus was only present for one task. Different stimuli were presented in different contexts. If the main benefit of specialization is that individuals do not waste time in transitioning between tasks, this particular experimental set-up would fail to measure any difference in efficiency between specialists and generalists. The author justifies the use of this set-up by arguing that allowing for different task stimuli to be simultaneously present would have led to individuals performing only the most urgent stimulus, thus shadowing their true task preferences. Nevertheless, competition between stimuli does occur in natural settings and a choice among different tasks must be made by individuals. On the other hand, the currency in which efficiency is measured, i.e., the time it takes for individuals to perform the task, may not reflect the actual benefit of worker specialization. The study of Dornhaus showed that specialized workers were responsible for the majority of the workload on the different tasks. This may be beneficial if we consider that workers spend energy in task performance. Thus, having specialists that take care of the bulk of the work for "their" task but avoid other tasks may allow the colony to save energy in the long run. The fact that specialists work comparatively more than generalists may also partly explain why they are not necessarily the fastest workers; maintaining a fast pace for a long time may be energetically expensive. More studies are required that use other measures of the benefits of specialization and consider the colony-level aspects of energy management.

In this context we must also consider the results of the fixed and reinforced threshold model (chapters 3 and 4, respectively), where we saw that division of labor evolved as a by-product of selection for other traits (worker distribution and minimization of idleness, respectively). It would be fruitful to study if reinforcement and learning are general processes in eusocial insects and their non-social related groups, or whether they are only specific to some groups. In solitary halictine bees, for example, there is no evidence of reinforcement (Jeanson et al. 2008).

Much work has been done on the interaction of individuals (e.g., Cole 1991, Huang & Robinson 1992, Powell & Tschinkel 1999, Gordon & Mehdiabadi 1999, Greene & Gordon 2007), but recently the possibility to track individuals in lab colonies throughout long periods of time has given new insights on the importance of specific individuals and their experience in the successful coordination and performance of tasks (Langridge et al. 2008, Robinson et al. 2009b). So far these studies have been largely limited to the ant *Temnothorax albipennis*, a crevice-nesting species with relatively small colonies and long-lived workers. It would be important to widen these studies to other species, to understand how worker-worker interactions affect species with other characteristics.

In general, empirical work on division of labor focuses on species which have advanced forms of division of labor, i.e., eusocial species. This is understandable, as we can find the most impressive examples of worker-worker communication and coordination in such species, such as the honey bee dance (Von Frisch 1974) and tandem-running in *Temnothorax* spp. (Franks & Richardson 2006). However, I would argue that to understand how division of labor evolved it is necessary to look at the forms of division of labor in species without such evolved forms of eusociality. We can perhaps find more clues in these organisms as to why division of labor is adaptive and how the first behavioral rules leading to division of labor look like.

Concluding remarks

The models presented in this thesis aim to fill a gap in the theory of division of labor, by integrating self-organization and evolution. I showed that the behavioral rules to which individuals obey are of great importance for the outcome of division of labor. Considering different behavioral rules and architectures yields quite disparate results. Nevertheless, these models are highly simplistic in terms of the complexity of colony life. Future models should use more mechanistic approaches to fitness, by considering clear-cut interpretations of the nature of tasks and their dynamics. A first attempt has already been made to model colony life in a more realistic fashion, by explicitly considering two general tasks, foraging and brood care, and how the performance of each task affects the other (A. Duarte, O. Ivanov, and F. J. Weissing, in preparation). The role of environmental variation should also be considered in the future, as it is crucial that colonies respond adaptively to environmental changes.

The models considered here are also simplistic in their consideration of behavioral architectures. Real social insects are likely to have much more complex architectures. However, it is important to note that increasing the complexity of the behavioral architectures in a model comes at the cost of losing comprehensibility, as results become more difficult to interpret. It should nevertheless be tested how much the complexity of the network affects the outcome of evolution.

Hopefully, the modeling approach used here will also inspire more empirical research that brings light to the potential benefits of specialization and to the behavioral mechanisms underlying task choice in eusocial insects.

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English summary

Division of labor

A common problem faced by members of a group that must cooperate to perform a set of tasks is how best to coordinate their activities. Should every individual try to tackle as many tasks a possible? Or should "task groups" form, whereupon different sub-groups specialize in different tasks? This division of labor is easily achievable in humans, where centralized control typically occurs: Allocating people to different tasks is the job of supervisors and managers. However, it is not immediately clear how division of labor can occur in other group-living organisms. And yet, some form of division of labor is often found in nature whenever different individuals must cooperate. How do individuals know what to do? A proximate explanation to the complex division of labor shown in some species invokes self-organization: Individuals obey to simple behavioral rules and through their interaction with other individuals and the environment a pattern of division of labor emerges in a self-organized manner. Our understanding of division of labor is not complete, however, without considering the evolutionary mechanisms that favor or suppress the existence of such behavioral rules.

An extreme example of division of labor occurs in the social insects. These organisms, which, among others, include bees, ants, wasps and termites, live in colonies of variable size. Characteristically, few individuals reproduce in these colonies (the "queens"), and the vast majority are non-reproductive individuals ("workers"). These workers are in charge of all the tasks related to colony growth and maintenance, such as foraging, brood care, cleaning the nest and defence. It is often found that different groups of workers tend to perform different tasks. Empirical research has shown that several factors are correlated with the probability of individuals to choose certain tasks: Age, morphology, genetics, developmental conditions and individual experience all seemingly play a role in determining which task individuals are likely to choose. Theoretical research has focused recently on the behavioral rules that may lead to self-organized division of labor in social insects. A number of models has been proposed, highlighting different types of behavioral rules.

In chapter 2 we review and classify the existing self-organization models according to the factors that promote individual differences in task choice. Broadly, differentiation can be seen as being driven by three different factors: spatial differentiation, signal-response dynamics and social interactions. Models that focus on spatial differentiation argue that individuals behave differently mainly due to the spatial distribution of tasks in a nest. While individuals have enough work to do on a specific task, they should not easily come across stimulus for another task. Models in which differentiation is driven by signal-response dynamics argue that the signals indicating task need in a colony are reduced by the performance of a task. One such model is the response threshold model, which encapsulates the following idea: If individuals possess different thresholds to start working on a task, then the individuals that have the lower thresholds will become the specialists for that task because they reduce the signal (or stimulus) to a level which falls below other individuals' thresholds. Models that focus on social interactions argue that information passed among colony members influences the decisions taken by individuals. These models do not consider how the different behavioral rules are shaped by natural selection. However, the few evolutionary models for division of labor do not consider the proximate mechanisms underlying specialization. We argue that unifying the self-organization and evolutionary perspective is important for predictions on the evolution of division of labor. It is not only important to identify which mechanisms are able to produce division of labor, but also in under what circumstances can these mechanisms evolve. An easy way to achieve a unifying model is to start from existing self-organization models and apply evolution to them, by considering that the outcome of interactions between individuals and their environment is an important fitness component (e.g., work performed in certain tasks). We identify the major benchmarks that should be achieved by this unifying framework. Namely, an evolved mechanism for division of labor should achieve: Emergent specialization and an adaptive distribution of workers over tasks; flexibility and developmental robustness; evolutionary stability and attainability. We also identify some of the challenges inherent to our approach.

Models

In chapter 3 we start from the existing response threshold model and allow for individual thresholds to evolve. In the original model, two groups were considered to exist in a colony, with opposing thresholds for different tasks. It is not surprising that division of labor emerges in these circumstances. The question arises whether threshold distributions capable of producing division of labor can evolve from scratch. We look at what happens to a population of colonies with homogeneous thresholds over evolutionary time under different fitness scenarios. In the standard fitness scenario, selection is strongest on the amount of work performed by the colonies. In an alternative fitness scenario, we consider stronger selection on the distribution of workers over tasks. In the standard fitness scenario, individual thresholds evolve to zero. In this circumstance, the response threshold model vanishes, in a sense, because all individuals are constantly active and willing to perform any task. When selection on the distribution of work over tasks is strong, however, and a 3:1 work ratio is favored, a low level of specialization evolves as a by-product of selection on the work distribution. However, the optimal work distribution of 3:1 was never achieved. In fact, we found that one of the limitations of the threshold model is that work distribution is largely determined by the parameters governing stimulus dynamics. We then considered a cost to task switching (in terms of time). In the standard fitness scenario, evolutionary branching occurred in both thresholds, and high levels of specialization evolved as the population became highly polymorphic. However, the level of specialization was dependent on the specific genetic composition of the colonies' parents, and a large part of the population still showed little specialization. Interestingly, the evolution of specialization was not made easier by allowing foundresses to mate multiple times. The results from this chapter illustrate that the assumptions of self-organization models can be severely shaken by explicit consideration of evolutionary mechanisms.

In chapter 4 we use the more flexible reinforced threshold model as a starting point. In this case, thresholds are not fixed throughout the lifetime of individuals, but can be reinforced with the performance of tasks. Under threshold reinforcement, an individuals' threshold decreases upon performance of a task (positive reinforcement), and increases upon not performing a task (negative reinforcement). We focused on the evolution of the reinforcement parameters (starting from a state of no reinforcement), under different conditions. First we considered a situation similar to the standard fitness scenario used in chapter 3. Second, we introduced a switching cost in the model. Third, we considered an effect of experience in performance efficiency. In the first case we found that a selective pressure for lower thresholds induces positive reinforcement and therefore low levels of worker specialization, even when there are no direct benefits to worker specialization. Direct selection on worker specialization, either through a switching cost or a positive effect of experience in performance efficiency, resulted in higher levels of specialization. In contrast to the fixed threshold model examined in chapter 3, when specialization evolved in the reinforced threshold model, it did so for all colonies in the population, suggesting that an experience-based task choice is more developmentally stable than a genetic-based task choice. Despite the seemingly more flexible mechanism, the limitations of the response threshold in terms of worker distribution were still observed.

Box 1 deals with an important implementation detail in response threshold models: the tie-breaking mechanism. When individuals are willing to perform either of two tasks, they must choose among them. Here I examine three different ways to implement task choice and avoid "ties" between tasks. A simple way is to not let individuals encounter two tasks at the same time; in this way, only one task at a time can be assessed. To this implementation I call "random task encounter", because individuals encounter one randomly selected task. An alternative is to consider that if individuals are willing to perform both tasks, one of them is then chosen at random ("tie-break by random choice"). Yet another option is to consider that individuals must perform the task for which the difference between task and threshold is largest ("tie break by largest difference"). I found that when task stimuli are perceived without noise, the third implementation, "tie break by largest difference", produces high levels of worker specialization in the absence of any selection on specialization and under restricted genetic variation. The difference between tie-breaking mechanisms in the level of specialization produced is reduced when there is noise in the perception of task stimulus.

Chapter 5 studies a more open type of behavioral architecture than the one encapsulated in the threshold model. For this purpose we use artificial neural networks and allow the parameters of the networks to evolve; the advantage of doing so is that a wider range of strategies can evolve, and we are not limited to the constraints of the response threshold mechanism. We compared two types of network architecture, one considering only feedforward connections (i.e., current experience does not affect future decisions), and another considering feedback of experience on future decisions. We focused again on worker specialization and worker distribution as the colony phenotypes of interest. We found that, contrary to the threshold mechanism, where a biased work distribution (different from 1:1) was difficult to obtain, feedforward neural networks always evolved a biased work distribution, even when this was not optimal. This was owing to selective pressures on minimizing idleness. Feedforward networks, in the presence of switching costs, could evolve only genetically determined specialization; hence, as in the threshold mechanism, colonies suffered a lack of specialization when parents were too genetically similar. The second type of network considered allowed for experience-based specialization to evolve, and thus all colonies in the population could develop specialization. The feedback network also allowed colonies to achieve the optimal work distribution under most conditions.

Empirical research

Differences between individuals in task choice could stem from their ability to detect levels of task-related stimuli. In chapter 6 we investigate the ability of ant antennae to detect task-related chemical stimuli, by using electroantennography on foragers and nurses of the ant Camponotus fellah. Electroantennography measures the electrical current generated by the triggering of olfactory and mechanical sensors in antennae. We exposed ant antennae to cuticular hydrocarbon extracts of larvae, nestmates, non-nestmates and 1-octanol. No difference was found between foragers and nurses in the response to the chemical stimuli presented, which indicates that task choice differences are related to processes occurring in the central nervous system. However, we did find that nurses' antennae tended to react more strongly to air flow than foragers' antennae. Larval cuticular hydrocarbons were not detected by antennae. Nestmate and non-nestmate cuticular hydrocarbons were detected but the latter elicited a stronger reaction, which suggests a recognition system based on the detection of alien compounds.

Conclusions

The theoretical models presented in this thesis show that unifying the self-organization and evolutionary perspective is crucial for a more complete understanding of division of labor. One of the take-home messages of this thesis is that parameter values in self-organization models that produce emergent division of labor do not always evolve if natural selection is allowed to take place. This highlights the importance of testing the evolutionary stability of behavioral rules. However, division of labor occasionally evolved in the absence of direct benefits of worker specialization, as a by-product of selection for other traits. Therefore, considering specific mechanisms can change evolutionary predictions. Overall we also found that genetically determined task choice (also called genetic task bias in the literature) is associated with a much higher variance in worker specialization and colony fitness. Behavioral architectures that allow for an effect of experience on future decisions produce a much more homogeneous population, with higher levels of worker specialization.

Nederlandse samenvatting

Arbeidsverdeling

Een veelvoorkomend probleem waartegen leden van een groep die moeten samenwerken om een set taken uit te voeren, aanlopen is de vraag hoe hun activiteiten het best kunnen worden gecoördineerd. Zou elk individu moeten proberen zoveel mogelijk verschillende taken aan te pakken? Of zou het beter zijn om subgroepen te vormen die zich specialiseren op verschillende taken? Deze arbeidsverdeling kan gemakkelijk bereikt worden bij de mens, waar meestal controle centraal plaatsvindt: het toewijzen van mensen aan verschillende taken is bijvoorbeeld vaak het werk van hooggeplaatsten en managers. Het is echter niet meteen duidelijk hoe een dergelijke arbeidsverdeling voor kan komen in andere organismen die ook in groepen leven. En toch, wanneer verschillende individuen moeten samenwerken in de natuur wordt er vaak wel een vorm van arbeidsverdeling gevonden. Hoe weten deze individuen wat ze moeten doen? Een proximate verklaring voor de complexe arbeidsverdeling die wordt gevonden in sommige diersoorten maakt gebruik van zelforganisatie: individuen gehoorzamen aan simpele gedragsregels en door hun interactie met andere individuen en met de omgeving ontstaat er vanzelf een patroon van arbeidsverdeling op een zelfgeorganiseerde manier. Ons begrip van arbeidsverdeling is echter niet volledig wanneer we de evolutionaire mechanismen die het bestaan van zulke gedragsregels bevorderen of onderdrukken buiten beschouwing laten.

Een extreem voorbeeld van arbeidsverdeling komt voor in sociale insecten. Deze organismen, waaronder onder andere bijen, mieren, wespen en termieten vallen, leven in kolonies van variërende grootten. Karakteristiek voor deze kolonies is dat slechts enkele indiviuen zich voortplanten (de “koninginnen”) terwijl de overgrote meerderheid uit steriele individuen bestaat (de “werksters”). Deze werksters zijn verantwoordelijk voor alle taken die te maken hebben met het groeien en onderhouden van de kolonie, zoals foerageren, broedzorg, het schoonmaken van het nest en verdediging van het nest tegen parasieten en indringers. Vaak wordt gevonden dat verschillende groepen werksters de neiging hebben verschillende taken uit te voeren. Empirisch onderzoek heeft aangetoond dat verschillende factoren gecorreleerd zijn met de kans dat bepaalde individuen bepaalde taken kiezen: Leeftijd, morfologie, genetica, de omstandigheden tijdens de ontwikkeling en individuele ervaring, lijken allemaal een rol te spelen in het bepalen van welke taken individuen met grote waarschijnlijkheid kiezen. Recentelijk heeft theoretisch onderzoek zich gericht op de gedragsregels die mogelijk leiden tot zelfgeorganiseerde arbeidsverdeling in sociale insecten. Een aantal theoretische modellen zijn voorgedragen, die zijn toegespitst op verschillende typen gedragsregels.

In hoofdstuk 2 geven we een overzicht van en classificeren we de bestaande zelforganisatiemodellen aan de hand van factoren die individuele verschillen in taakkeuze bevorderen. In het algemeen kan differentiatie worden gezien als gedreven door drie verschillende factoren: ruimtelijke differentiatie, signaal-respons dynamica en sociale interacties. Modellen die zich richten op ruimtelijke differentiatie voorspellen dat individuen zich voornamelijk verschillend gedragen vanwege de ruimtelijke verdeling van taken over het nest. Zolang individuen genoeg werk te doen hebben met een specifieke taak, zullen ze niet snel geprikkeld worden (oftewel een stimulus ontvangen) om een andere taak te doen. Modellen waarin differentiatie wordt gedreven door signaal-respons dynamica zeggen dat de signalen die de noodzaak voor een taak in een kolonie aangeven worden afgezwakt door het uitvoeren van de taak. Eén van deze modellen is het het 'respons-drempelwaarde-model', wat het volgende idee inhoudt: als individuen verschillende drempelwaarden hebben voor het beginnen aan een taak, dan zullen de individuen met de lagere drempelwaarden voor een taak specialisten voor die taak worden, omdat zij het signaal (of stimulus) afzwakken tot een niveau dat onder de drempelwaarde van de andere individuen valt. Modellen die gericht zijn op sociale interacties voorspellen dat de informatie die onder de leden van een kolonie wordt doorgegeven van invloed is op de besluiten die individuen nemen. Al deze modellen laten buiten beschouwing hoe de verschillende gedragsregels vorm worden gegeven door natuurlijke selectie. De weinige evolutionaire modellen voor arbeidsverdeling laten op hun beurt echter de proximate mechanismen die ten grondslag liggen aan specialisatie buiten beschouwing. Wij zijn van mening dat het belangrijk is om zowel het zelforganisatie perspectief als het evolutionaire perspectief samen te brengen voor het voorspellen van de evolutie van arbeidsverdeling. Het is niet alleen belangrijk om de mechanismen die arbeidsverdeling kunnen bewerkstelligen te identificeren, maar ook onder welke omstandigheden deze mechanismen kunnen evolueren. Een makkelijke manier om zo'n verenigend model te maken is om te beginnen met bestaande zelforganisatiemodellen en daar evolutie op toe te passen, daarbij aannemend dat het resultaat van de interacties tussen individuen en hun omgeving (bijvoorbeeld het werk uitgevoerd in bepaalde taken) een belangrijke fitness component is. Wij identificeren de belangrijkste referentiepunten die zouden moeten worden bereikt in deze samenbrengende aanpak . Een geëvolueerd mechanisme voor arbeidsverdeling zou namelijk het volgende moeten bereiken: emergente specialisatie en een adaptieve verdeling van werksters over taken; flexibiliteit en robuustheid in ontwikkeling; evolutionaire stabiliteit en haalbaarheid. We identificeren ook een aantal van de uitdagingen die inherent zijn aan onze aanpak.

Modellen

In hoofdstuk 3 beginnen we met het bestaande respons-drempelwaarde-model en laten we de individuele drempelwaarden evolueren. In het originele model werd aangenomen dat er twee verschillende groepen met tegenovergestelde drempelwaarden voor verschillende taken binnen één kolonie bestonden. Het is dan ook geen verrassing dat arbeidsverdeling onder deze omstandigheden ontstaat. Vervolgens komt de vraag op of de verdeling van drempelwaarden die in staat is om arbeidsverdeling te produceren vanuit het niets kan evolueren. Daartoe kijken we wat er over evolutionaire tijd gebeurt met een populatie kolonies met homogene drempelwaarden onder verschillende fitness scenario's. In het standaard fitness scenario werkt natuurlijke selectie het sterkst op de hoeveelheid arbeid die is uitgevoerd door de kolonie. In het alternatieve scenario werkt natuurlijke selectie het sterkst op de verdeling van werksters over taken. In het standaard fitness scenario evolueren individuele drempelwaarden naar nul. In zekere zin verdwijnt het respons-drempelwaarde-model dan, omdat alle individuen constant actief zijn en bereid zijn om welke taak dan ook uit te voeren. Echter, als natuurlijke selectie vooral van invloed is op de verdeling van werksters over taken en een 3:1 werkverhouding de grootste hoeveelheid nakomelingen oplevert, evolueert er een zwakke arbeidsverdeling als bijproduct van selectie op de verdeling van werk. De ideale werkverdeling van 3:1 wordt echter nooit bereikt. Deze analyse legt één van de belangrijkste beperkingen van het drempelwaardemodel bloot, namelijk dat de verdeling van arbeid voornamelijk wordt bepaald door parameters die de stimulus dynamica reguleren, terwijl de acties van de werkers zelf weinig consequenties hebben voor de werkverdeling. Vervolgens keken we naar de situatie waarin het wisselen van taak kosten met zich meebrengt voor werksters in termen van tijd. Onder het standaard fitness scenario komt evolutionaire splitsing voor, waarbij de distributie van beide drempelwaarden zich vertakken en hoge niveaus van specialisatie evolueren in een zeer polymorfe populatie. Het niveau van specialisatie was echter afhankelijk van de genetische samenstelling van het ouderpaar van de kolonie en in een groot deel van de populatie kwam bovendien nog steeds maar weinig specialisatie voor. Interessant genoeg werd de evolutie van specialisatie niet bevorderd door koninginnen toe te staan meerdere keren te paren. De resultaten van dit hoofdstuk laten zien dat de aannames van zelforganisatiemodellen stevig kunnen worden opgeschud door het expliciet in beschouwing nemen van evolutionaire mechanismen.

In hoofdstuk 4 gebruiken we het flexibelere 'zelfversterkende drempelwaarde'-model als startpunt. In dit geval behouden drempelwaarden niet dezelfde waarde gedurende de levensduur van een individu, maar kunnen ze versterkt worden door het uitvoeren van bepaaldetaken. In een dergelijk scenario van drempelwaardeversterking wordt de drempelwaarde van een individu kleiner naarmate het de taak vaker uitvoert (positive versterking) en groter naarmate de taak minder wordt uitgevoerd (negatieve versterking). We richtten ons op de evolutie van de parameters die dit zelfversterkend patroon bepalen in een populatie waar enige zelfversterking van deze drempelwaarden volledig afwezig is in het begin. We onderzochten een aantal verschillende scenarios: als eerste keken we naar een situatie die vergelijkbaar was met het 'standaard fitness' scenario uit hoofdstuk 3. Als tweede veronderstelden we bepaalde kosten voor het wisselen van taak toe aan het model. Als derde keken we naar de effecten van werkervaring op de efficiëntie van het uitvoeren van de taak. In het eerste geval vonden we dat selectiedruk op lagere drempelwaarden een positieve versterking induceert en daardoor leidt tot lage niveaus van specialisatie in werksters, zelfs als er geen directe voordelen zijn van werksterspecialisatie. Directe selectie op werksterspecialisatie, zij het door kosten voor het wisselen van taak, zij het door een positief effect van ervaring op taakefficiëntie, resulteerde in hogere niveaus van werksterspecialisatie. In het geval dat specialisatie evolueert, vonden we specialisatie in alle kolonies in de populatie, in tegenstelling tot het vaste-drempelwaardemodel (zie hoofdstuk 3) waar specialisatie alleen in bepaalde kolonies voorkwam. Dit suggereert dat taakkeuze die is gebaseerd op ervaring stabieler is dan genetisch bepaalde taakkeuze. Ondanks dit schijnbaar stabielere mechanisme, zagen we nog steeds dezelfde limitaties van het respons-drempelwaarden-model in termen van werksterverdeling. Box 1 behandelt een belangrijk detail in de implementatie van de respons-drempelwaarde-modellen: het *tie-breaking* mechanisme. Wanneer individuen bereid zijn om beide van twee taken uit te voeren, moeten ze tussen de taken kiezen. Hier onderzocht ik drie manieren om taakkeuze te implementeren en gelijke bereidwilligheidom beide taken uit te voeren ("*ties*") te voorkomen. Een simpele manier is om individuen niet twee taken op hetzelfde moment te laten tegenkomen; op deze manier kan er maar één taak per keer beoordeeld worden. Deze implementatie noem ik "willekeurige taak ontmoeting", want individuen komen maar één willekeurig geselecteerde taak tegen. Een alternatief is om individuen één taak willekeurig te laten kiezen ("*tie-break* door willekeurige keuze"), wanneer individuen bereid zijn beide taken die ze tegenkomen uit te voeren. Nog een andere optie is dat individuen de taak moeten uitvoeren waarbij het verschil tussen de taak en de drempelwaarde het grootst is ("*tie-break* door grootste verschil"). Ik heb gevonden dat wanneer taakstimuli worden ontvangen zonder ruis, de derde implementatie ("*tie-break* door grootste verschil") hoge niveaus van werksterspecialisatie bewerkstelligt, mits selectie op specialisatie afwezig is en genetische variatie in drempelwaardeniveaus laag is. Het verschil tussen de verschillende *tie-breaking* mechanismen in het niveau van specialisatie dat bereikt werd, is kleiner wanneer er stochastische ruis zit in het ontvangen van de taakstimulus.

Hoofdstuk 5 bestudeert een opener type van gedragsarchitectuur dan hetgene wat werd verondersteld in het drempelwaardemodel. Om dit te bereiken, gebruiken we kunstmatige neurale netwerken en laten we de parameters van het netwerk evolueren; het voordeel hiervan is dat een grotere verscheidenheid aan strategieën kan evolueren en dat we de beperkingen vermijden van het respons-drempelwaarde-model. We vergeleken twee typen netwerkarchitectuur: het eerste type netwerk heeft alleen feedforward verbindingen had (dat wil zeggen dat huidige ervaringen toekomstige beslissingen niet beïnvloeden), terwijl het tweede type netwerk een feedback veronderstelt tussen ervaring en toekomstige beslissingen. We richtten ons wederom op werksterspecialisatie en werksterverdeling als de koloniephenotypen waarin we geïnteresseerd waren. We vonden dat, in tegenstelling tot het drempelwaardemodel waarin een scheve werkverdeling (anders dan 1:1) moeilijk te bereiken was, er in feedforward neurale netwerken altijd een scheve werkverdeling evolueerde, zelfs wanneer dit niet optimaal was. Deze scheve werkverdeling werd veroorzaakt door selectiedruk op het minimaliseren van situaties waarin geen werk wordt gedaan. Feedforward netwerken kunnen alleen op genetisch niveau bepaalde waarden van specialisatie evolueren, in de aanwezigheid van kosten door het wisselen van taak. Hierdoor leden kolonies aan een gebrek aan specialisatie wanneer de kolonieouders genetisch teveel hetzelfde waren, net zoals in het respons-drempelwaardemodel. Het tweede type netwerk waar we naar keken stond toe dat specialisatie gebaseerd op ervaring (in plaats van genotype) kon evolueren, zodat alle kolonies in de populatie in staat waren specialisatie te ontwikkelen. Het feedback netwerk liet kolonies ook de optimale werksterverdeling bereiken onder de meeste omstandigheden.

Empirisch onderzoek

Verschillen tussen individuen in taakkeuze kunnen komen door verschillen in hun vermogen om taakgerelateerde stimuli te detecteren. In hoofdstuk 6 onderzoeken we het vermogen van mierenantennen om taakgerelateerde chemische stimuli to detecteren, met het gebruik van electroantennografie op foeragerende werksters en werksters die voor de larven zorgen, alle van de mier Camponotus fellah. Electroantennografie meet de electrische spanning die gegenereerd wordt door stimulatie van geur- en mechanische sensoren in de antennen. Wij stelden mierenantennen bloot aan koolwaterstofextracten van het cuticulum van larven, nestgenoten, niet-nestgenoten en 1-octanol. Er werd geen verschil gevonden tussen foeragerende werksters en werksters die voor de larven zorgen in hun respons tot de chemische stimuli die werden gegeven. Dit toont aan dat verschillen in taakkeuze gerelateerd zijn aan processen in het centrale zenuwstelsel. We vonden echter wel dat de antennen van larve-verzorgende werksters sterker reageerden op luchtstroming dan antennen van foerageerders. De koolwaterstofextracten uit de cuticula van larven werden niet gedetecteerd door de antennen. Koolwaterstofextracten uit de cuticula van nestgenoten en niet-nestgenoten werden wel gedetecteerd, zij het dat de laatste een sterkere reactie opriepen. Dit suggereert dat het herkenningssysteem gebaseerd is op het detecteren van niet-eigen substanties.

Conclusies

De theoretische modellen die in dit proefschrift zijn gepresenteerd laten zien het bijeenbrengen van het zelforganisatie perspectief en het evolutionaire perspectief cruciaal is voor een beter begrip van arbeidsverdeling. Eén van de lessen die te leren zijn uit dit proefschrift is dat parameterwaarden van zelforganisatiemodellen die emergente arbeidsverdeling bewerkstelligen, niet altijd evolueren wanneer natuurlijke selectie toegestaan wordt plaats te vinden. Dit benadrukt het belang van het testen van evolutionaire stabiliteit van gedragsregels. arbeidsverdeling evolueerde echter ook af en toe in de afwezigheid van een direct voordeel van werksterspecialisatie, als een bijproduct van selectie op andere kenmerken. Daarom kan het in beschouwing nemen van verschillende mechanismen evolutionaire voorspellingen veranderen. Over het algemeen vonden we ook dat genetisch bepaalde taakkeuze (ookwel genetische taakvoorkeur genoemd in de literatuur) is geassociëerd met veel hogere variatie in werksterspecialisatie en koloniefitness. Gedragsarchitecturen die een effect van ervaring op toekomstige beslissingen toestaan produceren veel homogenere populaties, met hogere niveaus specialisatie.

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